Stressor response and spatial dynamics of mountain lake communities

by

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Abstract

Multiple novel and rapidly changing environmental factors (i.e. anthropogenic stressors) are increasingly affecting ecological communities, and their functional roles in ecosystems. Consequently, freshwater biodiversity has declined worldwide; however, the functional impacts of this loss should be contingent upon local species' traits and the potential for tolerant species to compensate for sensitive taxa. In a metacommunity (i.e. a set of local communities connected regionally by species dispersal) context, stressor resistance may further depend on the arrival of stress-tolerant colonists from the regional species pool. My research, in collaboration with international colleagues, combines quantitative literature review, a manipulative field experiment, and innovative multivariate analyses of continental-scale observational data to address scientific knowledge gaps concerning the impacts of multiple stressors on freshwater communities.

First, a meta-analytic approach was used to assess the tendency for freshwater stressors to interact by comparing the independent and combined effects of paired stressors across 286 experimental responses from 88 published articles. The nature of multiple stressor interactions is a key source of uncertainty for conservation practitioners, as co-occurring stressors may generate unanticipated non-additive interactions (i.e. ecological surprises) that either dampen or amplify their individual direct effects. Net impacts of stressors varied, but were less than expected (i.e. antagonistic) overall, indicating a potentially high degree of co-adaptation to stressors within freshwater ecosystems. Further, aggregate functional properties of communities were less sensitive than biodiversity, suggesting that compensation by stress-tolerant species may frequently lessen the functional consequences of co-occurring environmental changes.

Among the greatest threats to freshwater ecosystems are climate change and biological invasions. There is also growing evidence to suggest that cold-adapted mountain lake communities are uniquely sensitive to warming and impacts from exotic sportfish, which have been introduced to create angling opportunities around the world. To explore potential interactions among invasive fish, higher temperatures, and importation of a regional species pool, I conducted a large outdoor mesocosm experiment introducing rainbow trout to planktonic communities collected from fishless alpine lakes. Fish introduction exerted strong negative impacts on prey species richness and biomass production, which were relatively unaffected by warming. However, importation of fish-tolerant species from neighbouring lakes rescued local alpine zooplankton communities from the adverse predatory effects of exotic salmonids. These findings indicated that native species' traits mediate the impacts of invasive species and highlighted the importance of maintaining habitat connectivity to buffer against future stressors.

Finally, I compiled and analyzed historical zooplankton records for 1,234 waterbodies across the North American Cordillera, from Yukon Territory, Canada, to California, USA, to evaluate the hierarchical importance of fish introduction and climatic factors among the multiple covarying local and regional drivers of continental-scale biodiversity patterns. Spatially structured local environmental factors (climate, catchment features, and fish stocking history) explained more variance in species composition than the degree of connectivity among sampled sites or their geographic variables. Further, the inferred effects of species sorting and dispersal processes varied based on species' traits. These findings highlighted the greater sensitivity of mountain lake communities to local catchment and climate conditions than dispersal limitation, and the importance of terrestrial–aquatic linkages and fisheries management under a changing climate.

My doctoral research provides several novel insights into the impacts of multiple stressors on ecological communities, with clear implications for the conservation of freshwater resources. I discovered that stressor interactions are frequently antagonistic, and using mountain lakes as a model ecosystem, I found that species' traits play an important role in mediating metacommunity assembly and stressor response along geographic gradients. By integrating experimental and observational evidence, my thesis demonstrates a rigorous scientific approach to identifying the functional consequences of global change.

Preface

Here, my thesis reflects publications and a submitted manuscript prepared in collaboration with fellow researchers. Citations for individual studies and author contributions are as follows.

A version of Chapter 2 has been published as: Jackson MC, Loewen CJG, Vinebrooke RD & Chimimba CT. (2016) Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology*, 22, 180–189. As denoted in the final published version of the paper, Jackson MC and I contributed equally to this work and share lead authorship. Jackson MC conceived of the idea for this study and initiated data compilation. We both contributed substantially to data collection and manuscript composition; however, my role involved greater contributions to study design and data analysis/interpretation. Vinebrooke RD and Chimimba CT provided conceptual input and manuscript revisions.

A version of Chapter 3 has been published as: Loewen CJG & Vinebrooke RD. (2016) Regional diversity reverses the negative impacts of an alien predator on local species-poor communities. *Ecology*, 97, 2740–2749. I designed the study, conducted the experiment, enumerated zooplankton samples, analyzed the data, and composed the manuscript. Vinebrooke RD conceived of the idea and contributed to study design and manuscript revisions. All animal use followed care protocols approved by the University of Alberta Biosciences Animal Care and Use Committee (Study Title: Cumulative impacts of invasive salmonids and global warming on fishless alpine lake ecosystems, ID No.: AUP00000670, Approved: May 12, 2013).

A version of Chapter 4 has been submitted for publication as: Loewen CJG, Strecker AL, Larson GL, Vogel A, Fischer JM & Vinebrooke RD. (2017) Environmental and connectivity drivers of lake metacommunities along the North American Cordillera. I conceived of the idea and design of this study, assembled the database (i.e. reviewed literature and collected historical records), conducted all statistical and spatial analyses, and composed the manuscript. Strecker AL and Vinebrooke RD provided feedback on study design and data interpretation. All authors contributed historical data and/or manuscript revisions.

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I thank my supervisor, Rolf Vinebrooke, for his support and confidence these past years. His guidance has been immensely valuable to my development as a scientist, and I am grateful to have had this opportunity to work in his lab. I also recognize Mark Poesch and Suzanne Tank for their constructive contributions serving on my supervisory committee. I am indebted to the many individuals who provided field/lab assistance, contributed to formative discussions, or permitted access to historical resources, including Mohamad Youssef, Megan MacLennan, Mark Graham, Mitchell Johnson, Alex McClymont, Blake Stuparyk, Victoria Lemmons, Devin Lyons, Lauren Bortolotti, Laura Redmond, Caroline Feischl, Guy Chilton, Brian Curtis, Leslie Sikora, Rebecca Lofgren, Ben Wright, Robert Hoffman, Patricia Haggerty, David McIntire, and David Donald. I also appreciate the contributions of my coauthors, Michelle Jackson, Christian Chimimba, Angela Strecker, Gary Larson, Allan Vogel, and Janet Fischer.

Lastly, I offer thanks to friends and family for their unwavering support. In particular, I owe a debt of gratitude to my wife, Christine Robichaud, for her companionship and perpetual encouragement. I am grateful of her many contributions to my work, from assisting in the field to proofing abstracts and indulging frequent conversations on such topics as statistics and ecological theory. I would also like to recognize my parents, Ken and Alison Loewen, for founding my early education – and inspiring my fascination with nature and scientific inquiry.

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Chapter 1: Introduction

Research background and rationale

Global change in freshwater communities

At the current rapid pace of global change, multiple covarying environmental factors are increasingly affecting ecological communities (Crain et al. 2008, Darling & Côté 2008, Brown et al. 2013, Ban et al. 2014). These often novel and extreme anthropogenic perturbations (i.e. stressors), including climate warming and biological invasions, threaten native biodiversity (Pimm et al. 1995, Vinebrooke et al. 2004, Brook et al. 2008), with more drastic impacts often occurring in freshwaters than in terrestrial or marine ecosystems (Ricciardi & Rasmussen 1999, Sala et al. 2000, Jenkins 2003, WWF 2014). Freshwater ecosystems are particularly vulnerable to global change (Dudgeon et al. 2006, Ormerod et al. 2010) as they occupy low points on landscapes, integrating the effects of multiple local and regional processes (Williamson et al. 2009). Biodiversity conservation is critical; however, faced with the inevitable loss of freshwater species owing to multiple anthropogenic pressures, there is an essential and urgent need to fill scientific knowledge gaps concerning the functional consequences of global change and the mechanisms by which stressor resistance operate in aquatic communities (Hooper et al. 2005, Dudgeon et al. 2006).

The threats to global freshwater biodiversity are numerous. In addition to direct overexploitation of species from unsustainable harvest practices (WWF 2014), major stressors include contaminants (i.e. xenobiotics), acidification, nutrification, habitat alteration/degradation (e.g. physical manipulation, sedimentation, and altered hydrology), climate change (e.g. increasing temperature and ultraviolet radiation), and biological invasions (Sala et al. 2001, Dudgeon et al. 2006, WWF 2014). Recent attempts to curb global biodiversity losses have been hindered by deficient or misallocated efforts and largely failed to achieve international targets (Tittensor et al. 2014). Effective ecological management necessitates knowledge of both the types of stressors affecting communities and their relative consequences. For instance, biological invasions have been identified as one of the greatest threats to biodiversity and ecosystem functioning globally (Vitousek et al. 1997, Sala et al. 2000, Pimentel et al. 2004);

however, difficulties predicting invasion impacts, which are frequently context dependent, have diminished the success of invasive species management (Byers et al. 2002, Hulme et al. 2013, Ricciardi et al. 2013, Simberloff et al. 2013). An improved predictive understanding of the impacts and hierarchical importance of ecological stressors is vital for enhanced prioritization of sparse conservation resources.

Multiple stressor interactions

A key source of uncertainty in global change scenarios is the propensity for stressors to interact so as to mediate their individual direct effects (Sala et al. 2000, Brook et al. 2008). Interactions among multiple concurrent stressors are of critical importance because they may generate ecological impacts that differ markedly from the sum of their independent effects (e.g. Folt et al. 1999, Christensen et al. 2006, Harvey et al. 2013), yet they are often challenging to predict (Paine et al. 1998). Such frequently unanticipated interactions, or ecological surprises, modify the combined impacts of stressors either antagonistically (i.e. lessened impact) or synergistically (i.e. greater impact), depending on the similarity of their independent effects (Vinebrooke et al. 2004). For instance, if stressor impacts are highly redundant, then their combined effects on biodiversity should be less than additive, as both stressors should eliminate the same set of species. Conversely, synergy may occur where the effect of one stressor amplifies the impacts of another, exceeding thresholds or generating positive feedbacks that intensify species' vulnerabilities (Brown et al. 2008). While there is increasing evidence for the prevalence of non-additive interactions among stressors, particularly in marine ecosystems (Crain et al. 2008, Darling & Côté 2008, Harvey et al. 2013, Przeslawski et al. 2015), syntheses concerning freshwater ecosystems are lacking (but see Heugens et al. 2001, Darling & Côté 2008).

Biodiversity and functional traits

Biodiversity, a natural capital stock developed over billions of years of evolutionary trial and error, has tremendous cultural, aesthetic, scientific, and recreational value; however, a diversity of life also contributes vast benefits through the provision of various ecosystem goods and services (Costanza et al. 1997, de Groot et al. 2002, Hooper et al. 2005). Species diversity supports ecosystem functioning and resultant goods and services in several ways. For instance, numerical sampling effects (i.e. greater likelihood that important species are present) and positive complementary (i.e. increased niche partitioning) or facilitative species interactions may enhance resource use efficiency and increase ecological rates (Hooper et al. 2005, Cardinale et al. 2002). Biodiversity may also offer functional redundancy, whereby multiple species with similar functional roles contribute to the stability of ecosystem functioning over time (McCann 2000).

In the context of environmental change, functionally redundant species may differ considerably in their response to shifting conditions (termed response diversity; Elmqvist et al. 2003, Nystöm 2006). Therefore, more diverse communities should have greater biological insurance against ecological stressors, as tolerant species may compensate for sensitive taxa and buffer impacts to aggregate ecosystem properties (Loreau et al. 2001, Hooper et al. 2005). For instance, bee species with similar crop pollination functionality possess differing response traits mediating their interactions with important ecological stressors, such as land-use changes and pesticide application, indicating a potential for species abundance shifts to preserve community pollination services under changing landscapes (Williams et al. 2010). Similarly, a diversity of temperature tolerances among species in experimental protist communities supports greater biomass production under fluctuating temperature regimes (Leary & Petchey 2009). These examples illustrate the importance of species identity and response trait diversity, rather than species richness, for mediating the resistance of ecological communities. Identifying links between environmental change and key functional traits can reveal the potential magnitude of stressor impacts on native biodiversity, as well as their latent consequences for ecosystem functioning (e.g. Statzner & Bêche 2010, Darling et al. 2013, Mouillot et al. 2013).

Spatial dynamics of stressor resistance

By integrating the effects of local and regional processes, metacommunities (i.e. sets of local communities connected by species dispersal; Leibold et al. 2004) provide a flexible framework for considering the cumulative effects of multiple stressors. In this context, local communities share a regional species pool and are shaped by spatial dynamics in addition to more localized environmental filters (i.e. abiotic conditions controlling species occurrence) and biotic interactions (Amarasekare 2008, Kraft et al. 2015). Here, high immigration rates from neighbouring communities (i.e. mass effects) can prevent local extinctions where species are poorly suited (Leibold et al. 2004). In contrast, dispersal limitation may prevent species from arriving or establishing at locations where they might otherwise thrive (Bohonak & Jenkins 2003). In the absence of barriers, dispersal among local communities should allow species to colonize new habitats and track changing environmental conditions (Urban et al. 2011). These spatial dynamics emphasize relationships between local and regional factors of metacommunities and demonstrate their importance for the maintenance of local community functioning.

Species sorting along environmental gradients, whereby regional species colonize localities suiting their ecological niches (including breadth of stressor tolerances), provides an important means of community adaptability (Leibold et al. 2004). The spatial insurance hypothesis suggests that environmental heterogeneity, and a correspondingly diverse regional species pool, should impart resistance to stressed local communities by providing stress-tolerant colonists (Loreau et al. 2003). However, to mitigate the consequences of ecological stressors, tolerant regional species must first arrive and establish at impacted communities. Although often perceived as isolated islands, lake communities maintain connectivity by the exceptional dispersal abilities of many resident species (Bohonak & Jenkins 2003). In particular, the passive transport of desiccation-resistant propagules by wind and animal vectors (including waterbirds and human visitors) permits frequent dispersal of planktonic organisms (Vanschoenwinkel et al. 2008, Frisch et al. 2007). Such spatial dynamics may contribute to stressor resistance in lake metacommunities by facilitating opportunities for species with varying environmental tolerances to access novel habitats and functionally offset local impacts.

Community assembly along geographic gradients

Metacommunity boundaries are typically vague and may extend to continental scales for long-distance dispersers (Viana et al. 2016, Heino et al. 2017). Although dispersal probabilities inherently decrease with increasing distance between habitats (Heino et al. 2015), waterbirds permit dispersal of several aquatic species, including plankton, over hundreds of kilometers – particularly along major migratory routes such as the Pacific Flyway (Viana et al. 2013). Given sufficient time, chance dispersal of planktonic organisms should permit species sorting in relation to environmental conditions over broad geographic extents (e.g. Viana et al. 2016, Heino et al. 2017). However, the hierarchical importance of dispersal relative to the various climatic factors and local lake characteristics (including presence of invasive species and linkages with terrestrial habitats) driving species composition at large spatial scales is often obscured by spatial variation (i.e. autocorrelation) among environmental filters, and thus difficult to separate (Legendre 1993, Dray et al. 2006). Carefully devised experiments can be used to isolate individual mechanisms and provide strong inference on the basis of hypothesis testing (Platt 1964), but manipulative studies are also inherently limited in their ability to reflect the complexities of natural ecosystems (Quinn & Dunham 1983). As such, matching experimental findings with prudent analysis of observational data provides a means of verifying ecological hypotheses regarding the causes of broad-scale biodiversity patterns and the implications of global change.

Mountain lakes as a model ecosystem

Mountain regions provide unique opportunities to evaluate species diversity patterns over highly heterogeneous landscapes, as environmental conditions (e.g. climate and land cover) change rapidly along elevation gradients (Rahbek 1995, Lomolino 2001). Mountains are also the source of headwaters and often located within protected areas (Kollmair et al. 2005). These attributes make mountain lakes useful model ecosystems for studying the subtle effects of regional biodiversity drivers with minimal confounding anthropogenic influence (e.g. human land-use). Further, mountain regions are experiencing increased warming relative to lower elevations, especially at higher latitudes (Bradley et al. 2004, Nogués-Bravo et al. 2007, Pepin et al. 2015), and thus cold-adapted mountain lake communities are practical sentinels for the effects of global climate change (Williamson et al. 2009). North American mountain lakes have also been widely impacted by exotic salmonid stocking programs to enhance angling opportunities (MacCrimmon 1971, Crawford & Muir 2008). Knowledge of the impacts of these non-native sportfish relative to other local and regional factors of lake metacommunities, and their potential interactions with other stressors (e.g. climate warming), is important for informing fisheries management and may offer valuable insights into how native communities respond to invasive predators in a rapidly changing world.

Research objectives

Chapters 2–4 are versions of published or submitted manuscripts addressing the following research objectives:

Research objective 1 (chapter 2): Synthesize the existing primary scientific literature to uncover the nature of multiple stressor interactions in freshwater ecosystems.

a) Quantify the cumulative mean interaction type and frequency of interaction types across studies.
b) Assess how the net effects of multiple stressors vary among response metrics, levels of biological organization, organism types, and specific combinations of stressors.

Research objective 2 (chapter 3): Test experimentally for the effects of exotic trout on fishless alpine lake zooplankton communities and interactions between native species diversity and impact resistance.

a) Assess how invasion impacts differ in the context of climatic warming.
b) Advance our understanding of the scale-dependency of ecological insurance (i.e. local versus regional resistance).
c) Investigate the components of biodiversity important for biotic resistance (i.e. species richness versus species identities and underlying functional traits).
d) Explore the functional consequences of invasive predators and the use of functional trait–impact associations for predicting the magnitude and direction of stressor impacts.

Research objective 3 (chapter 4): Disentangle the hierarchical importance of environmental and spatial factors driving zooplankton composition patterns in mountain lake communities observed across the North American Cordillera.

a) Assess the degree of spatial structure in species variance at a continental scale.
b) Rank the consequences of climatic factors, catchment/lake features, and fish stocking history over broad geographic gradients.
c) Infer the relative importance of species sorting versus dispersal limitation in shaping the composition of local communities.
d) Examine links between key functional traits and metacommunity factors.

e) Unravel the sensitivity of mountain lakes communities to global change, including climate warming and sportfish introduction, and the implications of species traits for functional resistance.

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Chapter 2: Net effects of multiple stressors in freshwater ecosystems: a meta-analysis

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Introduction

The rise of ecological surprises in the primary scientific literature highlights the growing uncertainty over the cumulative impacts of multiple novel and extreme environmental changes (i.e. stressors; e.g. Paine et al. 1998, Christensen et al. 2006, Lindenmayer et al. 2010, Dehedin et al. 2013, Harvey et al. 2013). There is increasing evidence from marine environments that these stressors, such as rising temperatures, biological invasions, and habitat destruction, act synergistically to exacerbate biodiversity loss and ecological degradation (Crain et al. 2008, Harvey et al. 2013, Przeslawski et al. 2015). Interactions among stressors are at the core of these unexpected net ecological impacts (Sala et al. 2000) as they can generate complex effects that lessen or amplify the direct single effect of each stressor. The reported prevalence of non-additive effects of stressors across many marine ecosystems (Crain et al. 2008, Darling & Côté 2008, Harvey et al. 2013, Przeslawski et al. 2015) attests to an urgent need to fill knowledge gaps in freshwater ecosystems (Root et al. 2003, Ormerod et al. 2010, Staudt et al. 2013, Hering et al. 2015).

Empirical evidence of the net effects of multiple stressors on freshwaters remains very limited (but see Christensen et al. 2006, Darling & Côté 2008, Mantyka-Pringle et al. 2014) despite their impacts often being greatest on freshwater biodiversity (Jenkins 2003, WWF 2014). Freshwater ecosystems are particularly vulnerable to global change (Dudgeon et al. 2006, Ormerod et al. 2010) as they often occupy low points in landscapes, integrating the effects of local catchment and regional atmospheric processes (Williamson et al. 2009). In comparison, recent meta-analyses of the marine literature show that the net impact of multiple stressors are frequently either greater than (i.e. a synergistic interaction; Crain et al. 2008, Harvey et al. 2013, Przeslawski et al. 2015) or equal to (i.e. an additive effect; Ban et al. 2014, Strain et al. 2014) the sum of their single effects. Net effects of two or more stressors that were less than the potential additive outcome (i.e. an antagonistic interaction) were less common. Such variation in the net effects of stressor combinations depends in part on how impact is measured, as different biological receptors will inherently vary in their responsiveness to environmental change (termed response diversity; Elmqvist et al. 2003). For example, compensatory species dynamics within a stressed community may result in measurable changes in biodiversity while muting changes in function (e.g. primary production; Vinebrooke et al. 2003).

Theoretical models that predict the combined impact of stressor pairs on populations or communities are often based on an evaluation of the similarity of their independent impacts (Vinebrooke et al. 2004). For instance, if stressors A and B are highly redundant and both extirpate or negatively influence the same set of species in a community, then their net impact on species richness or functional performance (e.g. productivity or abundance) can be less than the sum of their independent effects (an antagonistic interaction). In contrast, synergy between stressors A and B can occur if species are affected, or thresholds are exceeded, only upon exposure to both stressors, resulting in their combined impact being greater than the sum of their single effects (a synergistic interaction). If stressor A affects a different set of species than stressor B, then their net impact on the community can equal the sum of their direct effects (an additive effect). In some cases, the net effect of stressors A and B may actually be in the opposite direction (positive or negative) than predicted based on their independent effects (Piggott et al. 2015). For instance, Christensen et al. (2006) found that warming reversed the positive effect of acidification on phytoplankton. We term such interactions reversals, perhaps representing the greatest of all ecological surprises.

Here, we synthesize findings from dual-stressor studies in freshwater ecosystems to address two main questions: (i) what is the cumulative mean interaction and frequency of interaction types across all studies? and (ii) how do interactions vary among response metrics and stressor pairs? We also focused on how higher temperatures associated with climate change interact with other key stressors to impact ecosystem properties. We used a meta-analytical approach to optimize our ability to both conduct a powerful quantitative test of the nature of interactions between stressors affecting freshwater ecosystems and identify testable hypotheses (Gurevitch et al. 2000, Parmesan et al. 2013, Hillebrand & Gurevitch 2014).

Materials and methods

Data search and selection criteria

To identify papers reporting an influence of multiple stressors on freshwater ecosystems we searched the ISI Web of Knowledge database (http://apps.isiknowledge.com) between July 2013 and March 2014 for the key word combination: (“synerg*” or “antagon*” or “additive” or “combined” or “multiple” or “factorial” or “experiment”) and (“freshwater” or “river” or “stream” or “lake”) and (“impact” or “effect”). In total, approximately 11,000 papers were screened for our study. We only considered those papers that investigated quantifiable effects of stressors independently and in combination compared to a stressor-free control, in nature or under experimental conditions. We only used papers that reported on the effects of extreme or novel manipulations of environmental conditions (i.e. stressors) rather than natural disturbances or interactions (e.g. competition or predation) with native species. Reported stressors included acidification, higher temperatures, ultraviolet radiation (UVR), contamination (xenobiotics or salinity), nutrification, habitat alteration (physical manipulation, sedimentation, altered flow regime or drought), and invasive species. Data were acquired directly from text and tables, from figures using Data Thief software (Tummers et al. 2010), or by contacting the corresponding authors (see Appendix A-1 for full list of data sources).

We use the term observation to refer to individual responses used in our analyses, and the term paper to refer to their source documents. In several cases, multiple observations were extracted from individual papers when either several experiments were conducted (i.e. using different sets of species, study locations, or stressor combinations) or various organism groups were measured (i.e. producers, invertebrates, or vertebrates). If not appropriately summarized at the organism group level (e.g. producer), observations were extracted on distinct functional groups (e.g. phytoplankton and periphyton). If a study examined the impact of multiple stressors experimentally over time, we only collected the longest time period (before complete mortality). When stressor recovery was included in the study, we used the final sampling point before the recovery period. If a study examined the effect of different degrees of stress (e.g. low and high nutrient enrichment) we only considered the most severe scenario (i.e. high nutrient enrichment), with the exception of studies where the most extreme scenario caused 100% mortality in response organisms; in these cases, we used the second most severe scenario. Several ecotoxicology studies tested the effects of a toxicant across a wide range of temperatures; in these cases, we compared ambient temperatures (usually defined in the papers) to warming of 4−10 ºC, based on warming predictions by the Intergovernmental Panel on Climate Change (IPCC 2013). Experiments consisted of laboratory/microcosm studies (taking place inside), mesocosm studies (taking place in outdoor tanks) and *in situ* studies (taking place in natural systems).

We considered the following response currencies or metrics: (i) survival, (ii) growth/size, (iii) condition, (iv) reproductivity, (v) behaviour, (vi) total biomass/abundance, (vii) diversity, and (viii) leaf decomposition. We included leaf decomposition as it is an important aspect of freshwater ecosystem functioning and was measured in several of our selected papers. If the response of an organism group to dual stressors during a single experiment was assessed using multiple metrics (e.g. plant biomass and plant diversity), we treated each as an independent observation only for inclusion in our full dataset. The full dataset was used for our full global random effects meta-analysis and our mixed effects response metric analyses (detailed and pooled; Table 2.1). Our full dataset initially contained 318 observations; however, we excluded 32 observations where the calculated predicted net effects were deemed impossible (see *Effect size calculation and interpretation* below for details). Thus our full dataset was reduced to 286 observations.

For the remainder of our comparisons, we excluded all diversity metrics (n = 31) and reduced our dataset to include only the most inclusive response metric per experiment for each organism group. For experiments where multiple response metrics were reported, the most inclusive response metric was selected where community responses were preferred over population or organism-level responses, and metrics were selected in favour of biomass/abundance over survival, survival over growth/size, growth/size over condition, condition over reproductivity, and reproductivity over behaviour. If the same experiment measured impact separately on multiple organism groups (e.g. producers and invertebrates), then each observation was retained. This reduced, most inclusive response metric, dataset (n = 230) was used for the majority of our meta-analyses (i.e. those not specifically comparing response metrics; Table 2.1) to minimize data non-independence. For each observation, we extracted mean, standard deviation, and sample size values for each treatment combination (stressor A;

stressor B; stressor A and B; no stressor control). We also retained relevant categorical data (e.g. location and response metric) for each observation.

Table 2.1 Meta-analytic models with details of category levels (where $n \geq 8$) and datasets used.

Model	Categorical levels	Dataset
1) Full global model	---	Full ($n = 286$)
2) Detailed response metrics	Animal survival; animal growth/ size; plant growth/ size; animal condition; animal biomass/ abundance; plant biomass/ abundance; animal diversity; plant diversity; leaf decomposition	Full ($n = 286$)
3) Pooled response metrics	Diversity; functional performance	Full ($n = 286$)
4) Reduced global model	---	Reduced ($n = 230$)
5) Response level (i.e. level of biological organization)	Community; population; organism	Reduced ($n = 230$)
6) Organism group	Vertebrate; invertebrate; producer	Reduced ($n = 230$)
7) Stressor-pair	Contamination × Habitat Alteration; Contamination × Invasion; Contamination × Nutrification; Contamination × Warming; Habitat Alteration × Nutrification; Invasion × Invasion; Invasion × Nutrification; Nutrification × UVR; Nutrification × Warming; Warming × UVR	Reduced ($n = 229$*)

Note: each meta-analytic model treats observation ID as a random effect; dashes denote meta-analytic model is non-categorical; reduced dataset is the most inclusive response metric dataset; and * denotes one observation dropped from model because stressor-pair was not replicated.

Effect size calculation and interpretation

Interaction effect sizes were calculated for each observation in our dataset using Hedges *d*, an estimate of the standardized mean difference not biased by small sample sizes (Gurevitch & Hedges 2001). The interaction effect size for each observation was calculated by comparing the null predicted additive effect to the actual observed effect of both stressors. Each interaction effect size was therefore based on the absolute difference between the observed net impact of dual stressors against a hypothetical additive outcome based on the sum of their single independent effects. For each mean response variable (*X*) from the four treatment groups (i.e. control (u), stressor A (A), stressor B (B) and both stressors A and B (AB)), the predicted additive effect (X_p) was calculated as:

$$X_p = (X_A - X_u) + (X_B - X_u) + X_u$$

At this stage, we removed any studies from our dataset (*n* = 32) where the predicted effect was deemed impossible (e.g. survival greater than 100% or biomass less than zero). Hedge's *d* effect sizes were then calculated for each observation by comparing the predicted additive effect with the actual observed effect of both stressors applied in combination (*AB*, *o*):

$$\frac{X_o - X_p}{S} j$$

where *j* is a weighting factor based on the number of replicates (*n*), calculated as:

$$1 - \frac{3}{4\left(n_o + n_p - 2\right) - 1}$$

S is the pooled standard deviation, calculated as:

$$\sqrt{\frac{(n_o - 1)\sigma_o^2 + (n_p - 1)\sigma_p^2}{n_o + n_p - 2}}$$

and the predicted standard deviation (σ_p^2) was calculated by pooling σ_A and σ_B and the pooled sample size (n_p) was calculated as $n_A + n_B$. Finally, the variance (V_d) around each interaction effect size (*d*) was calculated as:

$$\frac{n_o + n_p}{n_o n_p} + \frac{d^2}{2(n_o + n_p)}$$

Because stressors may impart either negative or positive effects on biological receptors, we inverted the response direction (∓) of interaction effect sizes for which the predicted additive effects (X_p) were negative (i.e. where both single effects were negative, or if in opposing directions, where the negative effect had the higher absolute value; Piggott et al. 2015). This allowed us to compare interaction effect sizes regardless of their directionality (Piggott et al.

2015). As a result, an interaction effect size (*d*) of zero represents an exact additive effect of the two stressors (i.e. their combined impact is equal to the sum of their single effects), while a positive *d* denotes a synergistic interaction (i.e. a combined impact greater than the sum of their single effects) and a negative *d* reflects either antagonism or a reversal interaction (a combined impact less than the sum of their single effects; Fig. 2.1). To distinguish between antagonistic and reversal interactions, we compared the direction (negative or positive, relative to the control) of the observed response to both stressors applied in combination (X_O) with the direction of their predicted additive response (X_P), and assigned reversals where they were opposite. Interaction significance was assessed using 95% confidence intervals calculated around each effect size (from a *t*-distribution), such that any interactions with intervals crossing zero were deemed additive (Fig. 2.1).

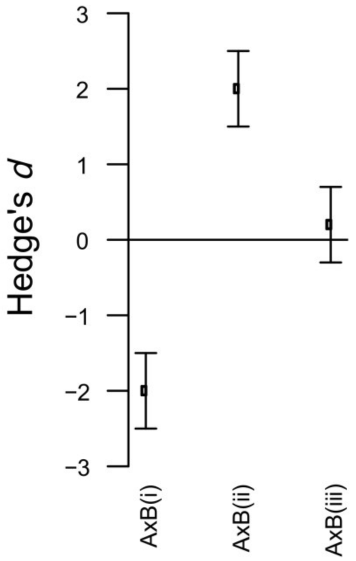

Fig. 2.1 The theoretical interactive effects of stressors A and B applied in combination, relative to their predicted additive response (= 0). Negative effect sizes (less than zero) represent antagonism or reversals (i) and positive effect sizes (greater than zero) represent synergistic interactions (ii), but only if their confidence intervals do not cross the x-axis. Interaction effect sizes with confidence intervals that overlap with zero were considered to be additive (iii).

Statistical analyses

Mean interaction effect sizes across studies were estimated from weighted meta-analyses. In each analysis, observation ID was treated as a random effect to account for the random component of effect size variation among observations, and inverse unconditional variance weights (w) were calculated for each interaction effect size as:

$$\frac{1}{V_d + \hat{\sigma}^2_{pooled}}$$

where $\hat{\sigma}^2_{pooled}$ is the pooled between-study/within-class variance estimated from the meta-analytic model (see Gurevitch & Hedges 2001 for further details of random/mixed model analysis). In addition to using random effects meta-analyses to assess the global mean interaction effect sizes across all observations included in our full and reduced datasets, we conducted a series of mixed effects meta-analyses where selected categorical moderators were treated as fixed effects to assess mean interactions at each categorical level (where $n \geq 8$; Table 2.1).

Using our full dataset, we conducted a detailed response metric analysis to evaluate the sensitivity of different response metrics to multiple stressors (Table 2.1). We followed this with a pooled response metric analysis, where response metrics were reassigned as either diversity (plant or animal diversity) or functional performance (all other response metrics), to assess the sensitivities of these broader response categories. We then used our reduced dataset to estimate mean effect sizes across receptor categories (response levels and organism groups) and stressor-pair combinations (Table 2.1). Percentile bootstrapped 95% confidence intervals (represented by the lowest and highest 2.5% of bootstrapped values) were calculated around each mean interaction effect size to assess significance (Fig. 2.1). Similar to the interpretation of interaction effect sizes for single observations, a positive mean effect reflects synergy, a negative mean effect reflects antagonism (reversals could not be distinguished with this method), and cases where the confidences intervals crossed zero were deemed additive.

In addition to the quantitative synthesis described above, we complemented each meta-analytic model with a vote-counting analysis to describe the frequencies of interaction types (including reversals) across individual observations. Randomization tests of independence

(Monte Carlo approximation using 9,999 permutations) were used to assess whether the frequencies of interaction types differed significantly among levels of each categorical moderator where $n \geq 8$ (Table 2.1). Randomization tests, rather than standard chi-square tests of independence, were used because of their utility for assessing data with small with group sample sizes and expected frequencies (Roff & Bentzen 1989). Interaction frequencies should be interpreted as the commonality of interaction types, as opposed to the mean interaction effect sizes obtained from our weighted meta-analytic models, which reflect the combined responses across studies. Therefore, smaller interaction effect sizes, which may frequently be assigned as additive in individual studies, may be revealed as non-additive by mean interaction effect sizes owing to greater statistical power.

Weighted meta-analyses were conducted in MetaWin Version 2.1 (Rosenberg et al. 2000) and the R computing program was used to perform independence tests (R Core Team 2016). To assess the robustness of our results, we conducted several additional analyses to investigate potential publication bias and the sensitivity of our findings to variation in sample sizes and effect size outliers (Appendix A-2). Although we found some evidence of asymmetry around our overall mean effect size estimate, we suspect this may be at least partially attributable to the considerable data heterogeneity observed. Nevertheless, the results of our sensitivity analyses indicate that our meta-analytic findings are robust to such variations.

Results and discussion

Stressor interactions across response metrics

We found 88 articles representing 286 separate observations (i.e. biological responses) to multiple stressors that met our selection criteria. In addition, 11 articles fitting our criteria were not included because we were unable to extract the data or the study did not report margins of error (listed in Appendix A-1). The majority of the research was carried out in North America (46 of 88 articles), followed by Europe (30) and New Zealand (7). All of the studies were conducted experimentally in laboratories (57), outdoor mesocosms (210), or *in situ* (19). Additional meta-analytic summary results (Table A-3.1) and heterogeneity estimates (Table A-3.2) are available in Appendix A-3.

Individual observations in our full dataset were most frequently antagonistic (40%; compared with 26% synergistic, 19% additive, and 15% reversed), and the mean interaction effect size across all responses was also significantly less than additive (i.e. antagonistic; Table A-3.1). Multiple stressors exerted significant antagonistic effects on animal abundance/biomass, animal condition, animal growth/size, animal survival, and plant diversity (Fig. 2.2a). Additive mean stressor effects were identified for the other four response metrics (decomposition, animal diversity, plant abundance/biomass, and plant growth/size; Fig. 2.2a).

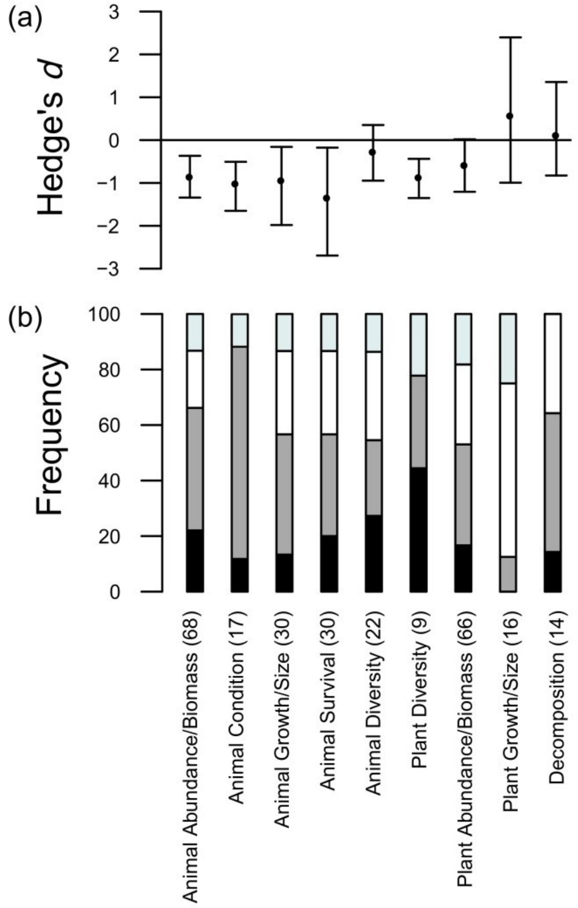

Fig. 2.2 The mean interaction effect sizes (Hedge's *d* and bootstrapped 95% confidence intervals; a) and frequencies (%) of interaction types (b) for different response metric categories. Interaction types are additive (black), antagonistic (dark grey), synergistic (white) and reversals (light grey). The number of observations/studies included in each category is indicated in parentheses. Mean responses are only presented where $n \geq 8$.

One possible explanation for widespread antagonism between freshwater stressors involves asymmetry of their single effect sizes. Here, the larger magnitude of the worst stressor completely overrides the effect of the weaker stressor, thereby negating its contribution to their net impact (Folt et al. 1999, Sala et al. 2000). The detected prevalence of antagonisms also suggests that exposure to one stressor often results in greater tolerance to the other (Vinebrooke et al. 2004). Here, a potential mechanism involves hard selection for tolerant organisms that are co-adapted to both stressors, thereby reducing their combined impact. Alternatively, acclimation to each stressor may involve the same behavioural or physiological mechanism, which would result in exposure to one stressor inducing greater tolerance against the other.

Frequencies of interaction types varied significantly ($\chi^2 = 40.36$; $P = 0.019$; df = 24; $n = 272$) and non-additive interactions were collectively more common than simple additive scenarios. Antagonisms occurred most often with animal condition (76.47%), synergies and reversals with plant growth/size (62.50% and 25.00%, respectively), and additive effects with plant diversity (44.44%; Fig. 2.2b). The highly variable nature of stressor interactions across these response metrics highlights the importance of currency selection when quantifying the net ecological impact of multiple stressors.

Stressors also exerted differing interactive and additive effects on functional performance and diversity responses, respectively. The mean interaction effect size for functional performance responses was antagonistic, while the mean effect of stressors on diversity was additive. Additive and reversal interactions occurred most frequently with diversity metrics (32.25% and 16.13%, respectively), while antagonistic and synergistic interactions occurred more frequently with functional performance metrics (41.57% and 27.06%, respectively); however, the frequencies of interaction types did not differ significantly ($\chi^2 = 4.87$; $P = 0.174$; df = 3; $n = 286$).

Compensatory species dynamics may explain the different mean interactive effects observed for stressor impacts on freshwater diversity and functional performance. The frequency of additive responses by diversity to dual stressors suggests that species eliminated by one stressor were often not the same that are eliminated by a second stressor. However, the prevalence of antagonism at the functional performance level suggests the remaining tolerant species may frequently compensate functionally for species loss, thereby reducing the net functional consequences of the stressors. Although the prevalence of functional species compensation has been debated in the literature (Houlahan et al. 2007, Gonzalez & Loreau 2009), several lines of evidence show it can help stabilize stressed freshwater communities (e.g. Klug et al. 2000 Fischer et al. 2001, Vinebrooke et al. 2003, Downing et al. 2008). Our findings suggest that functional resistance to stressors is not simply a function of biodiversity, but more often indicative of species identity and associated traits (e.g. Smith & Knapp 2003, Vaz-Pinto et al. 2013). Thus, functional resistance should be related to the response diversity of stressed communities (Elmqvist et al. 2003, Nyström 2006, Mori et al. 2013). As a result, our findings point to freshwater biodiversity being more sensitive than functioning to the cumulative impacts of multiple stressors.

Stressor interactions across receptor categories

For analyses of receptor categories and stressor pairs (see *Stressor interactions across stressor pairs* below), we considered only the most inclusive response metrics (i.e. the reduced dataset) to avoid pseudoreplication. As a result, our dataset was reduced to 230 observations for these analyses (Table 2.1). The majority of observations examined responses at the community level and the most frequently examined organisms were invertebrates (Fig. 2.3). The global mean interaction effect size was significantly antagonistic (Table A-3.1) and of the 230 observations considered, 94 (40.87%) were antagonistic, 64 (27.83%) were synergistic, and 34 (14.78%) were reversals, while 38 (16.52%) were additive.

The cumulative mean interaction effect of stressors was significantly antagonistic at the community and organism level but additive at the population level (Fig. 2.3a; Table A-3.1). However, the frequencies of interaction types did not differ significantly among levels of biological organization ($\chi^2 = 11.39$; $P = 0.074$; df = 6; $n = 230$). While antagonistic interactions were most frequent at the organism (65.22%) and community (40.88%) levels of biological organization, synergies and reversals occurred most frequently at the population level (37.14% and 17.14%, respectively), and additive interactions were most common at the community level (18.98%; Fig. 2.3b).

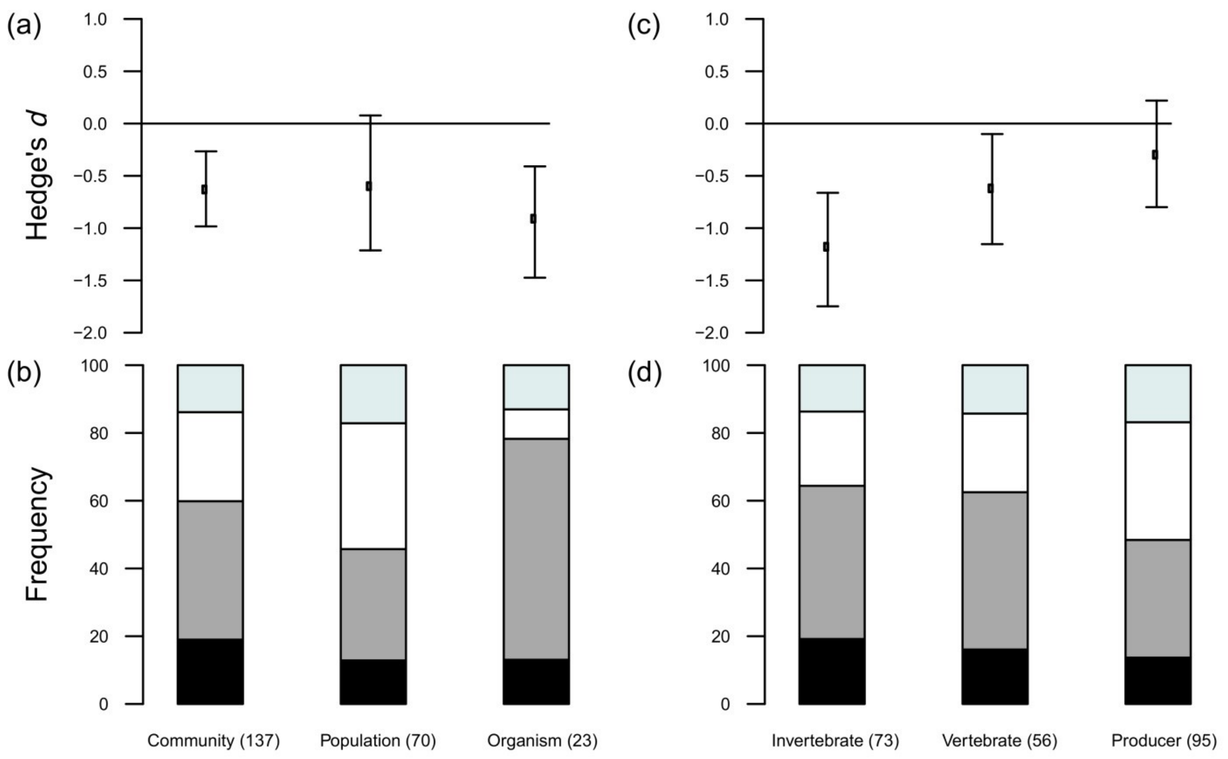

Fig. 2.3 The mean interaction effect sizes (Hedge's *d* and bootstrapped 95% confidence intervals; a, c) and frequencies (%) of interaction types (b, d) for different receptor categories, including level of biological organization (a, b) and organism group (c, d). Interaction types are additive (black), antagonistic (dark grey), synergistic (white) and reversals (light grey). The number of observations/studies included in each category is indicated in parentheses. Mean responses only presented where n ≥ 8.

Dual stressors exerted significant antagonistic effects on invertebrates and vertebrates, while primary producers responded in an overall additive fashion (Fig. 2.3c; Table A-3.1). However, frequencies of interaction types were similar across all organism groups ($\chi^2 = 5.70$; $P = 0.457$; df = 6; $n = 224$). Antagonistic responses occurred most frequently for invertebrates (45.21%) and vertebrates (46.43%), synergies and reversals were most common with primary producers (34.74% and 16.84%, respectively), and additive interactions most often affected invertebrates (19.18%; Fig. 2.3d). These results were surprising because sensitivity to global change is often thought to increase with trophic position (e.g. Crain et al. 2008, Petchey et al. 1999), particularly with warming, as metabolic demands increase faster than ingestion rates with higher temperatures (Vucic-Pestic et al. 2011). Here, the different responses of consumers and primary producers highlight the potential for multiple stressors to weaken trophic interactions and promote algal blooms. Many of the synergistic responses by primary producers involved net positive effects by stressors such as nutrification, UVR, and warming. In fact, 36 of the 64 synergistic interactions in our analysis were positive, and of these, 21 showed an increase in producer performance. Globally, correlative evidence suggests that nutrients and climate interact synergistically to increase the overall percentage of cyanobacteria in shallow lakes (Kosten et al. 2012). Experimental evidence supports these observations, showing warming and nutrient enrichment can exert a synergistic positive effect on phytoplankton growth (e.g. Doyle et al. 2005).

Stressor interactions across stressor pairs

Table 2.2 The number of stressor-pair observations meeting our data slection criteria (*n* = 230).

	Acidification	Contamination	Habitat alteration	Invasion	Nutrification	UVR	Warming
Acidification	0	3	2	0	0	3	5
Contamination		6	19	11	14	6	33
Habitat alteration			4	2	21	1	6
Invasion				13	10	0	7
Nutrification					0	10	41
UVR						0	13
Warming							0

Ten stressor pairs had sufficient observations ($n \geq 8$) for a comparison of their mean interaction effects (Table 2.2), which varied with their identity (Fig. 2.4a). Net effects were significantly antagonistic for contamination × invasion, contamination × warming, and warming × UVR; however, effects were additive for the remaining seven stressor pairs, including nutrification paired with warming, habitat alteration, invasion, and UVR (Fig. 2.4a). Although the frequencies of interaction types were not significantly different among stressor pairs ($\chi^2 = 28.25$;

$P = 0.402$; df = 27; $n = 185$), antagonistic effects occurred most frequently when warming occurred with UVR (61.54%), synergistic interactions occurred most often with nutrification and UVR (50.00%), reversal interactions were linked with warming and nutrification (26.83%), and additive interactions were common with paired invasions (30.77%; Fig. 2.4b).

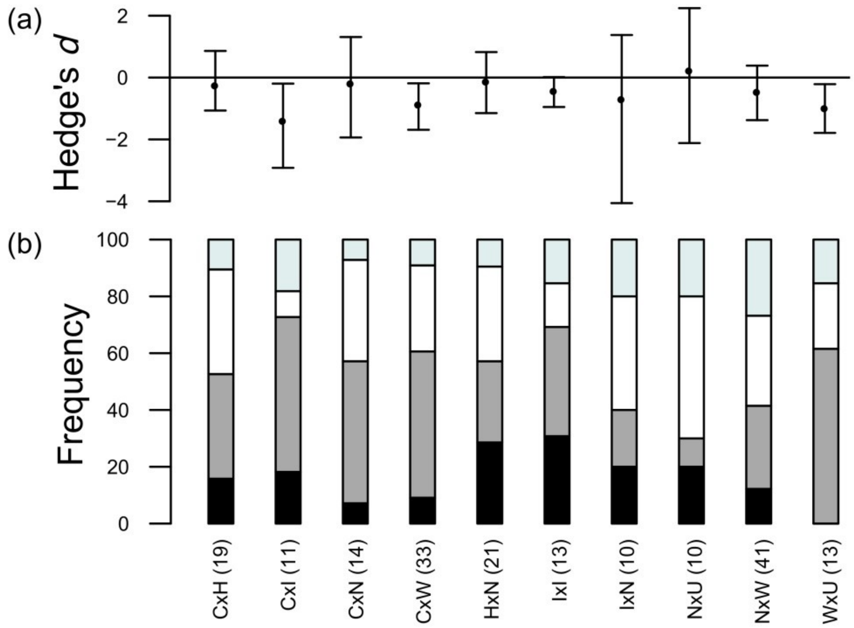

Fig. 2.4 The mean interaction effect sizes (Hedge's *d* and bootstrapped 95% confidence intervals; a) and frequencies (%) of interaction types (b) for different stressor-pair combinations. Interaction types are additive (black), antagonistic (dark grey), synergistic (white) and reversals (light grey). The number of observations/studies included in each category is indicated in parentheses. Mean responses only presented where $n \geq 8$. W = warming; C = contamination; H = habitat alteration; I = invasion; N = nutrification; and U = ultraviolet light radiation.

When higher temperature interacted with a second freshwater stressor, the mean interaction was antagonistic overall ($d = –0.68$; 95% CI = –1.1 to –0.3; $n = 105$). This finding is in contrast to studies of marine ecosystems where both Crain et al. (2008) and Harvey et al. (2013) found that warming most often interacted with a second stressor to produce a synergistic response. However, a recent re-analysis of the data presented by Crain et al. (2008) suggests that their original methods may have overrepresented synergies (Piggott et al. 2015). Furthermore, Ban et al. (2014) found that the mean effect of multiple stressors in coral reefs was additive overall, and it is important to note that different ecosystem types face different combinations of key stressors (Jenkins 2003, Pratchett et al. 2011). Lake (1990) suggested that benthic communities in freshwater and marine ecosystems may react differently to certain disturbances because of differences in the proportion of mobile versus sedentary biota. More general differences between freshwater and marine responses may be based on how specific stressors interact with inherent ecosystem properties. For example, Bancroft et al. (2007) predicted that UVR impacts should vary between marine and freshwater environments owing to differing optical qualities of the water; however, they were unable to detect significant differences from their meta-analysis. Additionally, the effects of some stressors (e.g. salinity and metal contaminants) may differ among freshwater and marine receptors based on physiological differences between biota (Hall & Anderson 1995, Heugens et al. 2001).

Higher environmental variability of smaller aquatic ecosystems may also foster greater species adaptation to stressors. Freshwaters generally experience much greater thermal variation than marine systems, so freshwater ectotherms might be better adapted to temperature changes than those from more thermally buffered marine ecosystems. For example, water fleas (*Daphnia* spp.) that are often focal species in lakes and ponds have been shown to be highly responsive (Colbourne et al. 2011) and capable of rapidly evolving in the face of environmental change (De Meester et al. 2011). Aquatic organisms also tend to be most sensitive to multiple-stressor effects near their thermal tolerance limits (Heugens et al. 2001), so more detrimental stressor interactions might be expected in marine ecosystems where species' ranges are often strongly aligned with their thermal limits (Pratchett et al. 2011, Sunday et al., 2012). Indeed, differences in how marine and freshwater ecosystems respond to similar stressors may depend on characteristics of the biological receptors and the environmental context, including the different communities, mechanisms, ecological networks, and abiotic conditions present (Bancroft et al. 2007, Tylianakis et al. 2008, Segner et al. 2014).

Three stressor-pair combinations had sufficient samples sizes for detailed analysis of interaction effects by level of biological organization or organism type ($n \geq 8$ for receptor categories within stressor pairs). The mean interaction effect size was significantly additive when nutrification was paried with warming or habitat alteration (Fig. 2.4a), regardless of level of biological organization or organism group. Contamination paired with warming had a significant antagonistic interaction overall (Fig. 2.4a) and at the organism level ($d = –0.77$; 95% CI = –1.3 to –0.3; $n = 10$); however, the interaction was additive at the population ($d = –1.27$; 95% CI = –3.6 to 0.4; $n = 11$) and community ($d = –0.26$; 95% CI = –0.7 to 0.2; $n = 12$) levels. Similarly, the mean interaction between contamination and warming became additive when considering only studies which measured impacts on vertebrates ($d = –0.26$; 95% CI = –1.0 to 0.5; $n = 12$). These results suggest that the type of organism and level of biological organization are both important in predicting the combined impacts of specific stressor pairs.

Reversal interactions as extreme ecological surprises

Reversal interactions (similar to the mitigating synergisms discussed by Piggott et al. 2015) were found in 34 of 230 observations (14.78%) from our reduced dataset. Although they were the least common type of interaction, reversals warrant special consideration because they reflect net effects that may differ markedly from those predicted by the typically assumed model of additivity (Piggott et al. 2015). Reversal interactions often involve the weaker of two stressors inverting the effect of the stronger. For instance, application of excess nutrients surprisingly reversed the toxic effect of atrazine on tadpoles as the additional resources likely permitted greater detoxification rates and stimulated growth, resulting in increased survival (Boone & Bridges-Britton 2006).

Our findings showed that the stressor most commonly associated with reversal interactions was warming (19.05% of warming interactions; Fig. 2.4b). The greater likelihood of reversal interactions when a stressor is paired with higher temperatures might be related to the stimulatory effect of warming. As nearly all biological activity increases with warming (Brown et al. 2004), temperature changes arguably have the greatest potential to mediate the effects of other more damaging stressors. For example, Thompson et al. (2008) found that warming reversed the negative effect of excess nitrogen supply on growth by alpine phytoplankton, possibly because higher temperatures stimulated enzymatic conversion of nitrate and ammonia. In contrast, Linton et al. (1997) showed that higher temperatures could reverse the stimulatory effects of sublethal ammonia enrichment on juvenile rainbow trout (*Oncorhynchus mykiss*) by increasing metabolic costs to where ammonia detoxification and growth rates were reduced. In these cases, warming directly altered the mechanisms by which the dominant stressors affected the biological receptors. However, like other non-additive scenarios, reversals may also manifest from complex indirect interactions (e.g. Messner et al. 2013). Given the complexity of ecological responses to temperature changes (Petchey et al. 1999, O'Connor et al. 2009, Dossena et al. 2012, Stendera et al. 2012) and their potential role in generating non-additive interactions with other stressors (Crain et al. 2008, Harvey et al. 2013), we might then expect even more ecological surprises in a warmer future.

Conclusions

We discovered a prevalence of antagonistic interactions between freshwater stressors across most receptor categories considered in our analysis (Table A-3.1). Thus, there may exist a high potential for co-adaptation within freshwater ecosystems to minimize the net effects of multiple stressors. Alternatively, antagonism may be attributable to a high degree of asymmetry in the magnitude of independent effects between freshwater stressors (Folt et al. 1999). In this case, ranking the worst stressor driving an antagonistic interaction would be essential to forecasting their cumulative impacts on a freshwater ecosystem (Sala et al. 2000, Piggott et al. 2015). However, our evidence of predominantly antagonistic responses by freshwater organisms should not lessen the need to reduce exposure to stressors as their net effects were still mostly negative. The urgency of these findings is underscored by a recent global assessment that compared multiple-stressor-induced average population declines of 76% among freshwater species to 39% among terrestrial and marine species since 1970 (WWF 2014).

Non-additive interactions characterized 83% (192/230) of the cumulative impacts of multiple stressors in our reduced, most inclusive response metric, dataset (81% or 233/286 in our full dataset). Mean interaction effect sizes varied significantly among stressor pairs and levels of receptor categories. Our analyses revealed different interactions for some stressor pairs (switching from antagonistic to additive, or vice versa) when only considering subsets of the data. This suggests that both stressor identity and characteristics of the ecological response (e.g. level of biological organization and organism type) are essential in predicting interactions between multiple stressors in freshwater ecosystems.

Our findings have implications for conservation management of freshwater ecosystems. For stressor pairs that generate additive or synergistic effects, management focusing on a single stressor should render a positive outcome (Brown et al. 2013). However, in communities affected antagonistically by stressor pairs, both stressors may need to be removed or moderated to produce any substantial ecological recovery due to positive co-tolerance (Brown et al. 2013, Piggott et al. 2015).

Our findings evoke several testable hypotheses for further investigation. Firstly, the observed trend of stressor synergies increasing the productivity of primary producers suggests that higher temperatures, UVR exposure, and nutrient enrichment may jointly stimulate harmful algal blooms. Secondly, functional performance metrics appeared less sensitive overall than diversity metrics to dual stressors, highlighting the need for further investigation into the extent to which functional compensation occurs in stressed ecosystems. Thirdly, although we have demonstrated a clear predominance of antagonistic stressor interactions in freshwaters, further studies are needed to determine the specific underlying ecological mechanisms (e.g. asymmetry of stressor magnitudes, hard selection for co-adapted organisms, or similarity in behavioural or physiological acclimation). Finally, perhaps most interesting is our finding that multiple stressor interactions differ between freshwaters and marine ecosystems and, although we have suggested several potential explanations, more research is needed to elucidate the specific physiological, genetic, or environmental drivers behind these differences.

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Chapter 3: Regional diversity reverses the negative impacts of an alien predator on local species-poor communities

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Introduction

Spatial processes play a central role in driving ecosystem dynamics (Massol et al. 2011) and shaping the outcome of biotic interactions (e.g. Cottenie & De Meester 2004, Howeth & Leibold 2010). For instance, species dispersal among local communities (i.e. metacommunities) affects food web structure and biodiversity by providing novel colonists or maintaining local populations via mass or rescue effects (i.e. a net influx of individuals preventing local species extinction; Loreau & Mouquet 1999, Leibold et al. 2004, Amarasekare 2008). By permitting access to the regional species pool, dispersal links local communities with broader regional processes, influencing their evolutionary and functional progression (Bohonak & Jenkins 2003).

Species immigration from neighboring habitats may also impart functional resistance to local communities against environmental change or anthropogenic stressors. As a source of biological insurance, biodiversity should buffer against the adverse functional consequences of species loss (Loreau et al. 2001, Hooper et al. 2005). Correspondingly, biodiversity across a heterogeneous landscape should impart resistance to stressed local communities via the colonization of tolerant individuals from a diverse regional species pool (i.e. spatial insurance; Loreau et al. 2003), though experimental evidence is limited (but see Thompson & Shurin 2012, Symons & Arnott 2013). In the context of invasive species, these insurance principles are similar to the biotic resistance hypothesis, which predicts that invaders exert less impact on more diverse communities (Elton 1958, Levine et al. 2004). However, trait variations among species may evoke markedly different responses to environmental change (Hooper et al. 2005). Therefore, community resistance should depend more on the identity of species and their functional diversity (i.e. positioning in functional trait space) than merely species richness (e.g. Daneshgar & Jose 2009, Mouillot et al. 2013). Knowledge of species-specific responses, and their underlying traits, is thus essential to predicting a stressor's impact.

Biological invasions are among the greatest threats to global biodiversity and ecosystem functioning (Vitousek et al. 1997, Sala et al. 2000, Byers et al. 2002, WWF 2014) and international efforts have been ineffective at reducing their ecological footprint (Tittensor et al. 2014). The limited success of invasive species management has often been attributed to challenges with predicting their impacts, which are frequently context dependent (Hulme et al. 2013, Ricciardi et al. 2013). Invasion effects may be mediated by characteristics of the recipient community (Ricciardi et al. 2013) or interactions with other environmental stressors (Ruiz et al. 1999, Jackson et al. 2016), such as climatic change (Rahel & Olden 2008). A better understanding of invasion impacts is urgently needed to inform and prioritize prevention and control measures (Byers et al. 2002, Hulme et al. 2013).

Mountain lakes are excellent venues for exploring the effects of regional species diversity on local communities as environmental heterogeneity along elevation gradients provides high regional diversity relative to species-poor local alpine communities (Rahbek 1995). There is a long precedent of stocking exotic sportfish in mountain lakes, which has aided the establishment of self-sustaining populations and impacted freshwater communities globally (MacCrimmon 1971, Knapp et al. 2001). There is also growing evidence that mountain regions are experiencing pronounced warming (Pepin et al. 2015), and that coldwater-adapted communities in high-elevation lakes are inherently sensitive to climate change (Parker et al. 2008, Battarbee et al. 2009). For instance, warming may reduce concentrations of large herbivorous zooplankton and subsequently increase primary production in alpine lakes (Holzapfel & Vinebrooke 2005).

To test for interactions among an alien predator, prey diversity, and warming, I conducted an experiment that involved introduction of the widespread invasive apex predator *Oncorhynchus mykiss*, a regional species pool of potential prey, and higher temperatures to a previously fishless local alpine lake zooplankton community. Here, I used a functional approach to test the hypothesis that, in the absence of dispersal limitation, access to a regional species pool lessens stressor impacts on local communities by increasing local response diversity (i.e. variation in functional traits associated with environmental tolerance). I also tested whether higher temperatures would modify (i.e. amplify or dampen) invasion impacts. Since visually feeding predators and higher temperatures are both expected to disproportionally suppress large-bodied species (Brooks & Dodson 1965, Moore & Folt 1993), I hypothesized that redundancy in their independent effects on community functional structure should yield less than additive net effects (i.e. an antagonistic interaction) when applied in combination.

Materials and methods

Experimental design

Outdoor mesocosms were established using 1,000-L translucent polyethylene tanks (~1 m^3) for eight weeks (July–September 2013) at the Barrier Lake Field Station, which is located at the eastern edge of the Canadian Rocky Mountains, Alberta, Canada (51°01′37″ N, 115°02′08″ W). Water from a nearby spring was collected and passed through a 250 µm mesh-size metal sieve to exclude macroinvertebrates before being used to fill the tanks. Zooplankton were obtained from three fishless alpine lakes by vertical hauls of each water column with a 63-µm-mesh conical net (see Table B-1.1 in Appendix B-1). These sites (Bighorn, Pipit, and Snowflake) were typical pristine alpine lakes, selected based on historical evidence of similar conditions (e.g. 2,226–2,353 m asl, 9.7–12.2°C early-summer surface temperature, 4–6 µg/L total phosphorous, and 0.5–0.8 mg/L dissolved organic carbon). Live zooplankton were immediately helicoptered to the field station and mixed in a 1,000-L holding tank. Equal aliquots of the assembled local species pool were then transferred to each of the mesocosms and left to equilibrate to tank conditions for 5-d prior to experimental manipulations. Mesocosms were open to the air by a 20 cm diameter opening, which was covered with 1 mm mesh-size covering.

Treatment application

All combinations of two crossed experimental treatments, each consisting of two levels, were replicated eight times for a total of 32 tanks. An invasion treatment was achieved by randomly assigning half of the tanks to receive a single *O. mykiss* fingerling obtained from a local hatchery (Ackenberry Trout Farms, Camrose, Canada). Introduced fish had a mean weight of 0.06 kg (SD = 0.02) and mean fork-length of 16.1 cm (SD = 1.8). Linear regression analyses showed that variation in fish weights did not significantly influence final zooplankton biomass ($P = 0.723$) or phytoplankton chlorophyll concentrations ($P = 0.985$). A warming treatment was achieved using four 300-W submersible heaters (Hagen, Montréal, Canada) per mesocosm to simulate 48-h heating events by amplifying daytime warming and sustaining elevated temperatures through the night. A pulsed warming protocol was chosen as few studies have examined the effects of climatic variability on alpine lake communities (Parker et al. 2008) despite expectations of increasing temperature extremes, particularly at higher elevations (Rangwala et al. 2012, Pepin et al. 2015). In addition, changes in thermal variation and extreme climate events (e.g. heat waves) frequently impact biota more than increasing mean temperatures (e.g. Smale & Wernberg 2013, Vasseur et al. 2014). Data loggers were deployed to record temperatures at 10 minute intervals in each tank for the entire experiment. The mean surface temperature difference between ambient (18.6° ± 2.5°C [mean ± SD]) and warmed mesocosms (20.1° ± 2.4°C) was 1.6°C; however, temperature differences ranged from 0°C to more than 6.0°C (see Fig B-2.1 in Appendix B-2).

After one month of stressor exposure, I applied a third factor (local vs. local + regional species pool) to determine whether regional colonists would rescue the local community by compensating for (i.e. offsetting) any loss of secondary production resulting from exposure to fish introduction or warming. The regional species pool treatment was achieved by inoculating half the mesocosms with individuals collected from 25 regional lakes and ponds in Banff, Yoho, Kootenay, and Peter Lougheed Mountain Parks (Table B-1.1). The sampled sites varied in their fish presence, near-surface temperature (10.4–21.5°C), elevation (1165–2687 m above sea level), and morphometry (e.g. total depth of <2.0–>20.0 m). Zooplankton were collected by either vertical or horizontal hauls (depending on depth and orientation of the water body) using a 63 µm mesh-size conical net and transferred daily to a 1000-L holding tank. Regional zooplankton were provided over two successive inoculations (Regional A on day 29 and Regional B on day 34), to increase lake coverage while minimizing time spent by live organisms in the intermediate holding tank, at concentrations of 18 and 9 µg/L, respectively. In total, the regional species pool provided 15 novel crustacean taxa, whereas the local species pool consisted of six species (Table 3.1). Larvae of the dipteran *Chaoborus* were also introduced as part of the regional species pool. Though important predators in many fishless montane lakes, low *Chaoborus* densities in the mesocosms (<0.1 organisms/L) likely limited their influence on zooplankton communities (see Fig B-3.1 in Appendix B-3). Tanks that did not receive a regional species pool treatment were provided an equal volume of heat-killed plankton to account for nutrient and water additions.

Table 3.1 List of taxa and functional traits.

Taxa/group	Code	Species pool	Motility	Feeding mode	Body size (mm)
Arctodiaptomus arapahoensis	Aara	Regional	Rapid	Filtration	1.25
Acanthocyclops vernalis complex	Aver	Local	Rapid	Raptorial	0.82
Acanthodiaptomus denticornis	Aden	Regional	Rapid	Filtration	1.46
Aglaodiaptomus leptopus	Alep	Regional	Rapid	Filtration	1.81
Bosmina longirostris	Blon	Regional	Slow	Filtration	0.35
Ceriodaphnia quadrangula	Cqua	Regional	Slow	Filtration	0.55
Chydorus sphaericus	Csph	Regional	Slow	Filtration	0.32
Daphnia spp.	DAPH	Local	Slow	Filtration	1.54
D. middendorffiana	---	Local	Slow	Filtration	---
D. pulex	---	Local	Slow	Filtration	---
D. mendotae	---	Regional	Slow	Filtration	---
D. dentifera	---	Regional	Slow	Filtration	---
D. Unidentified	---	Regional	Slow	Filtration	---
Diacyclops navus	Dnav	Regional	Rapid	Raptorial	0.81
Diacyclops thomasi	Dtho	Regional	Rapid	Raptorial	0.84
Diaphanosoma birgei	Dbir	Regional	Slow	Filtration	0.97
Eucyclops agilis	Eagi	Local	Rapid	Raptorial	0.86
Hesperodiaptomus arcticus	Harc	Local	Rapid	Filtration	2.50
Leptodiaptomus nudus	Lnud	Regional	Rapid	Filtration	1.16
Leptodiaptomus sicilis	Lsic	Regional	Rapid	Filtration	1.05
Leptodiaptomus tyrrelli	Ltyr	Local	Rapid	Filtration	1.24
Macrocyclops albidus	Malb	Regional	Rapid	Raptorial	1.28
Scapholeberis kingi	Skin	Regional	Slow	Filtration	0.56
Unidentified calanoid	UCAL	Regional	Rapid	Filtration	1.36
Unidentified cyclopoid	UCYC	Regional	Rapid	Raptorial	0.80
Calanoid copepodid	JCAL	Local	Rapid	Filtration	0.96
Cyclopoid copepodid	JCYC	Local	Rapid	Raptorial	0.58

Note: dashes indicate species value recorded at genus level.

Sample collection and processing

Crustacean zooplankton were collected immediately prior to the application of the treatments, to confirm that the starting communities were similar among tanks. Although some pre-treatment variation was observed (Fig. 3.1), differences in initial taxonomic richness and total biomass estimates were not significant (Table 3.2). Thereafter, samples were collected biweekly to permit assessment of treatment effects over time, while balancing sampling and enumeration constraints during the eight-week experiment. Zooplankton were collected by allowing 40-L of water to pass through a 63 μm mesh-size sieve from a spigot near the bottom of each mesocosm, while gently mixing the water column from above with a paddle. One tank was lost after day 14, and thus the factorial design was unbalanced for the remainder of the experiment (*n* = 3 for warming × fish present × local species only, but *n* = 4 for all other treatments). For the final sampling event (day 56), the remaining 840-L of water was sampled from each tank. All samples were immediately preserved in 70% ethanol.

Macrozooplankton (>250 μm) body counts and length measurements were conducted using stereoscopic microscopy (10–60x magnification). Length measurements were obtained for the first 25 detected specimens of each taxon to derive biomass estimates for each sample using length–weight regression (Dumont and Balvay 1979, McCauley 1984, Culver et al. 1985). Most zooplankton were identified to species (Edmondson 1959). Species traits were assigned based on generalizations of their taxonomic groups (Table 3.1). Cladocerans and copepods were assumed to differ based on their predator escape response, with copepod motility expected to be much faster owing to the use of their urosomes and multiple pairs of swimming legs (Williamson & Reid 2010). Similarly, cladocerans and calanoids were treated as selective suspension feeders while the generally more carnivorous cyclopoids were designated as raptorial/grasping feeders, as they actively orient themselves to attack their prey rather than passively obtaining food via currents (Barnett et al. 2007). Body sizes listed in Table 3.1 were obtained by averaging all length measurements for a given taxon, across the entire experiment. Methodological details for the concurrent sampling and analysis of algal samples are provided in Appendix B-4.

Table 3.2 Results of Poisson regression for taxonomic richness and analysis of variance for total zooplankton biomass over time.

Event and	Total taxonomic richness			Total biomass			
treatment	df	LR $\chi 2$	P (>$\chi 2$)	SS	df	F	P (>F)
Day 0							
F	1	0.000	1.000	<0.001	1	0.001	0.977
T	1	0.000	1.000	0.017	1	0.623	0.437
F x T	1	0.000	1.000	0.048	1	1.743	0.198
Error	28			0.769	28		
Day 14							
F	1	8.183	**0.004***	2.367	1	38.464	**<0.001***
T	1	0.028	0.867	0.019	1	0.302	0.587
F x T	1	0.250	0.617	0.001	1	0.002	0.964
Error	28			1.723	28		
Day 28							
F	1	23.439	**<0.001***	5.802	1	80.469	**<0.001***
T	1	0.001	0.978	0.013	1	0.177	0.677
F x T	1	0.009	0.925	0.008	1	0.117	0.736
Error	27			1.947	27		
Day 42							
F	1	6.097	0.014	1.438	1	41.542	**<0.001***
T	1	0.805	0.370	0.165	1	4.757	0.040
P	1	3.029	**<0.001***	1.125	1	32.481	**<0.001***
F x T	1	0.309	0.579	0.026	1	0.754	0.394
F x P	1	9.758	**0.002***	1.990	1	57.468	**<0.001***
T x P	1	0.513	0.474	0.001	1	0.038	0.848
F x T x P	1	0.141	0.708	0.015	1	0.437	0.515
Error	23			0.796	23		
Day 56							
F	1	2.451	0.118	0.058	1	0.452	0.508
T	1	0.009	0.924	0.048	1	0.377	0.545
P	1	61.780	**<0.001***	1.077	1	8.406	**0.008***
F x T	1	0.063	0.801	0.002	1	0.014	0.908
F x P	1	7.829	**0.005***	3.518	1	27.465	**<0.001***
T x P	1	0.540	0.462	0.006	1	0.043	0.838
F x T x P	1	0.254	0.615	0.019	1	0.150	0.703
Error	23			2.946	23		

Note: boldface type and * denote significance at $\alpha = 0.01$ (Bonferroni-adjusted alpha); LR $\chi 2$, likelihood-ratio chi-square statistic; and abbreviations are F = fish presence, T = temperature, and P = species pool.

Statistical analysis

To assess aggregate community responses to each treatment combination and test the hypotheses that local impacts are antagonistic and buffered by importation of a regional species pool, treatment effects on taxonomic richness and total community biomass were analyzed for each sampling date using Poisson regression and analysis of variance (ANOVA), respectively. Significance levels (i.e. α values) were adjusted from 0.05 to 0.01 using a Bonferroni correction to account for multiple comparisons. To assess treatment effects across individual taxa, the final community biomass distribution was analyzed by permutational multivariate analysis of variance (MANOVA; Wang et al. 2012). A non-parametric approach was used because MANOVA has been shown to lack robustness against multinormality, especially with low or unequal sample sizes (von Eye & Bogat 2004). Separate univariate linear regressions were fit for each taxon and summarized by a multivariate F statistic to assess the strength of treatment effects. The significance of treatment effects were estimated by performing 1,000 residual resampling iterations, accounting for correlation between response variables by shrinking the estimated correlation matrix (Wang et al. 2012). Multiple testing was applied to assess the significance of each taxon's response using the false discovery rate method to adjust P values (Benjamini & Hochberg 1995).

To test the hypothesis that stressor resistance is mediated by functional trait variation, interspecific trait–treatment associations were analysed using R-mode linked to Q-mode (RLQ) and fourth-corner analyses, in accordance with methodological refinements by Dray et al. (2014). RLQ analysis is a three-table ordination method that relates species traits to environmental factors by maximizing their covariance based on taxonomic performance across sites (Dolédec et al. 1996). First, taxa biomass by tank data were analyzed using correspondence analysis (L). Row (tank) and column (taxon) weights derived from the correspondence analysis were then used for multiple correspondence analysis of categorical treatment by tank data (R) and principal component analysis of functional trait by taxa data (Q), respectively. RLQ analysis subsequently combined these three separate ordinations (R, L and Q) to describe their joint structure by performing a double inertia analysis of R and Q, linked by L, which finds linear combinations of treatments and traits (RLQ axes) that maximize their covariance (Dolédec et al. 1996). Associations were evaluated visually after the global significance of the RLQ was assessed using a sequential two-model Monte-Carlo test with 49,999 permutations to test whether community biomass distribution was linked to both trait composition and experimental treatments (i.e. testing the L-R link by permuting tank vectors and the Q-L link by permuting taxon vectors; Dray et al. 2014). The significance of each bivariate trait–treatment association was then tested by fourth-corner analysis (Legendre et al. 1997), using similar sequential permutations (Dray et al. 2014).

All statistical analyses were conducted using R (R Core Team 2016). Parametric ANOVA tests were performed using the function 'anova' implemented in the 'car' package (Fox & Weisberg 2011), permutational MANOVA tests were performed using the function 'anova.manylm' implemented in the 'mvabund' package (Wang et al. 2012), and RLQ and fourth-corner analyses were performed using the functions 'rlq', ''randtest' and 'fourthcorner' implemented in the 'ade4' package (Dray & Dufour 2007). Taxa biomass data were $\log_{10}(x + 1)$ transformed prior to analysis to improve homoscedasticity and dampen outliers.

Results

Aggregate community response to stressors

Prior to importation of the regional species pool, introduced fish reduced significantly local taxonomic richness and total community biomass relative to controls (Fig. 3.1; Table 3.2). Thereafter, imported species offset significantly the fish effects (i.e. a fish–regional diversity interaction; Table 3.2). Specifically, imported species reversed the negative effect of fish on local taxonomic richness on days 42 and 56 (Fig. 3.1a). Similarly, amendment of the local communities with the regional species pool eliminated the negative effect of fish on total community biomass by day 42, and reversed the effect by day 56 (Fig. 3.1b). The warming treatment exerted neither significant direct or indirect community-level effects. In comparison, local taxonomic richness remained stable in the controls throughout the experiment (Fig. 3.1a) and total zooplankton biomass declined to ambient source lake concentrations (8.4–21.5 μg/L) by day 14 (Fig. 3.1b).

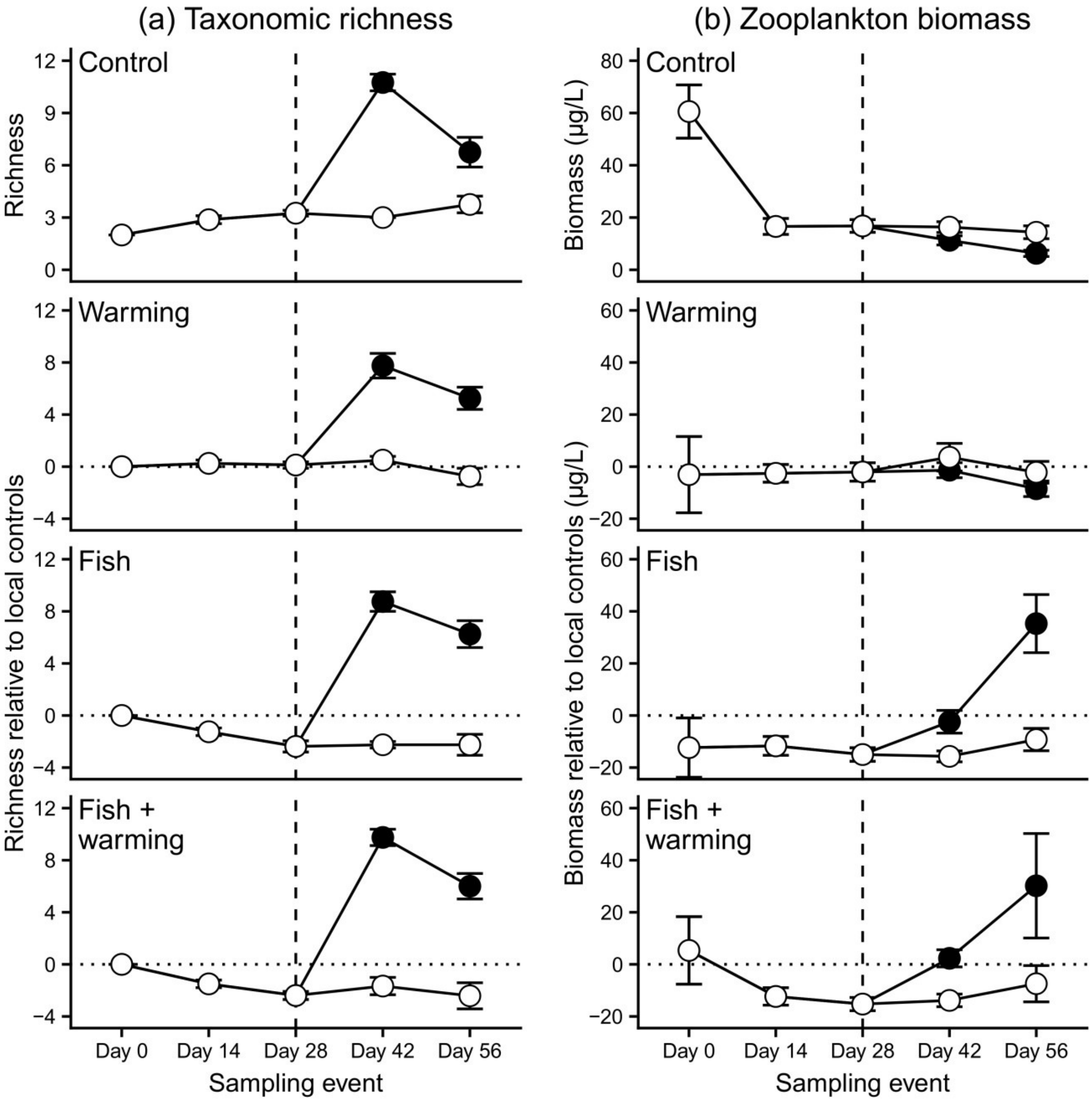

Fig. 3.1 Zooplankton (a) taxonomic richness and (b) total biomass over time. Stressor effects on local (white circles) and regional (black circles) communities were compared against stressor-free controls with local zooplankton species only. Vertical line represents application of regional dispersers. Data are mean values ± SE of the difference between sample means (*n* = 8 for days 0–28, except n = 7 for fish + warming on day 28; *n* = 4 for days 42–56, except *n* = 3 for fish + warming + local species only).

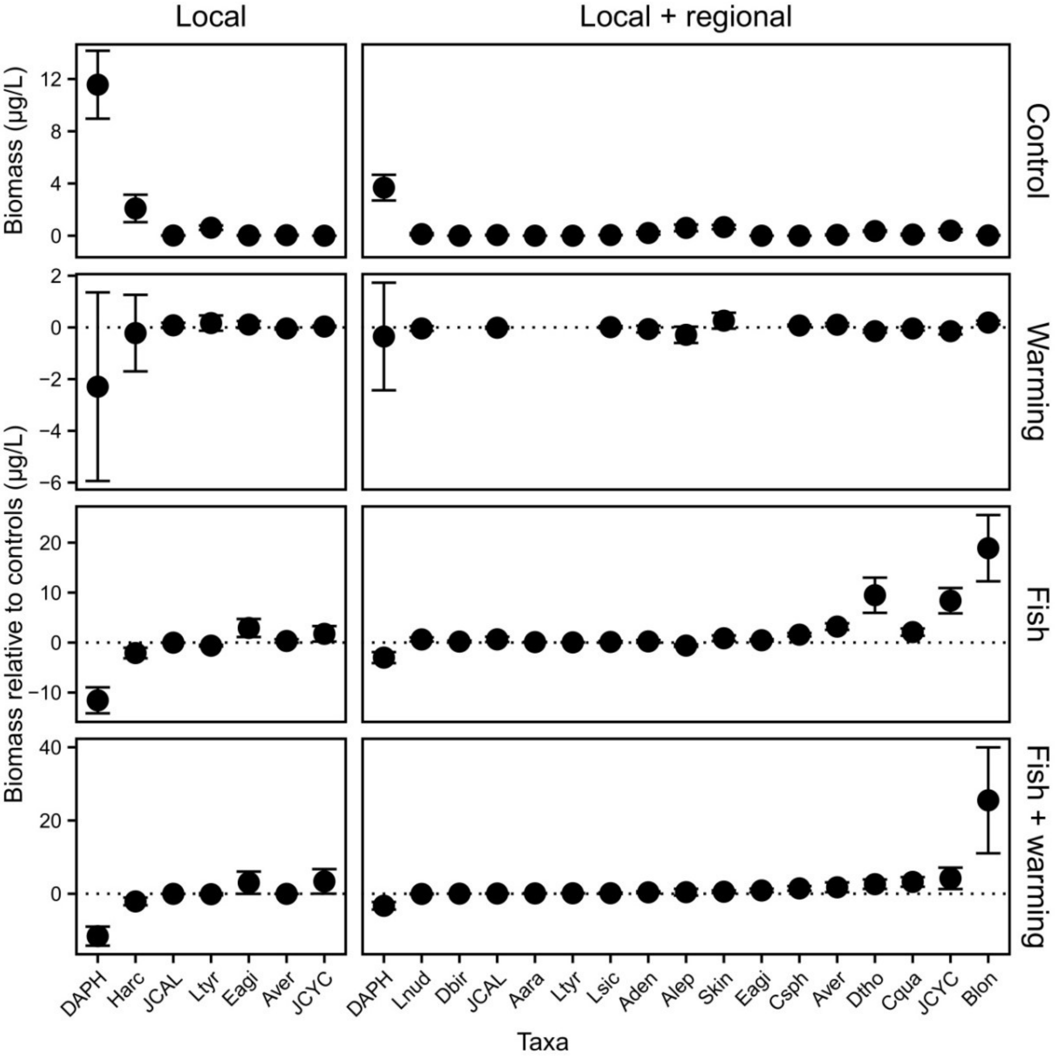

Fig. 3.2 Individual taxa biomass on the final sampling event. Stressor effects on members of the local and regional communities were compared relative to local and local + regional species pool controls, respectively. Taxonomic codes are defined in Table 3.1. Data are mean taxonomic responses from day 56 ± SE of the difference between sample means (*n* = 4, except *n* = 3 for fish + warming + local species only).

Community response diversity

The imported regional species pool also mediated the effects of introduced fish on the community biomass distribution (*P* = 0.001). In particular, amendment of the local alpine community with montane species increased the diversity of species responses to the presence of fish (Fig. 3.2). Fish suppressed larger alpine *Daphnia* spp. and *Hesperodiaptomus arcticus* while stimulating imported smaller montane cladocerans (*Bosmina longirostris* and *Ceriodaphnia quadrangula*) and cyclopoids (*Diacyclops thomasi* and *Acanthocyclops vernalis* complex; Fig. 3.2). The results of univariate tests of the effects of experimental treatments on individual taxa are reported in Tables B-5.1 and B-5.2 in Appendix B-5. None of the taxa were significantly affected by warming.

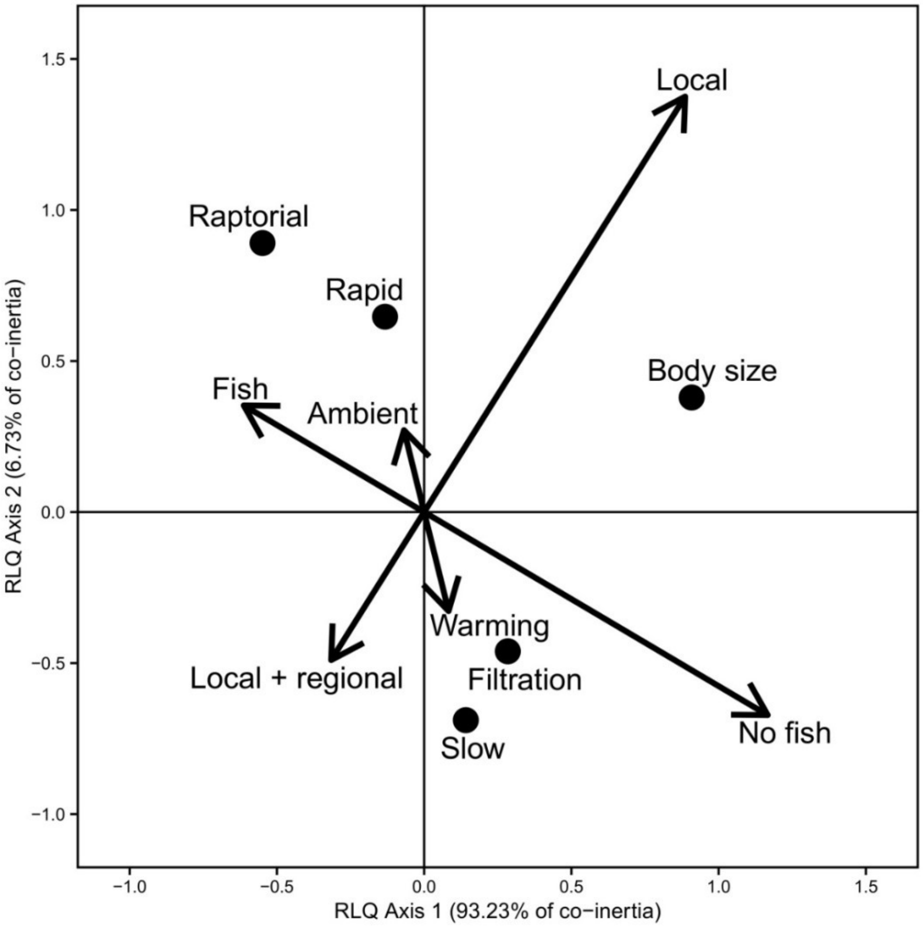

Fig. 3.3 R-mode linked to Q-mode (RLQ) biplot showing relationships between experimental treatments and zooplankton functional traits. Treatment effects, including fish presence (no fish or fish), temperature (ambient or warming) and species pool (local or local + regional), are presented as vectors (black arrows). Functional traits, including motility (slow or rapid), feeding mode (filtration or raptorial) and increasing body size, are presented as group centroids (black circles).

Functional trait–treatment associations

R-mode linked to Q-mode axis 1 captured 93.23% of the total association between traits and environmental treatments (i.e. co-inertia), accounting for the majority of their relation. The global RLQ model was deemed significant following the sequential testing of community biomass distribution links with experimental treatments ($P < 0.001$) and trait composition ($P = 0.022$). Summary statistics showed that RLQ axis 1 performed well in describing the covariance between the treatment matrix (R) and the trait matrix (Q; covariance = 0.894) while maintaining a strong correlation with the initial unconstrained ordination of sample scores (correlation = 0.676; Table B-5.3). Body size was significantly associated with fish presence and species pool ($P = 0.024$ for both; Table B-5.4). RLQ analysis associated increasing body size with the local alpine community under fishless conditions, and decreasing body size with importation of the regional species pool and introduced fish (Fig. 3.3). Similarly, raptorial feeding and rapid motility were associated, albeit non-significantly, with local communities exposed to fish and ambient temperatures; while filter-feeding and slow motility were most prevalent in regionally amended local communities under warmed, fishless conditions (Fig. 3.3).

Discussion

I discovered that importation of a regional species pool assembled from an environmentally heterogenic region could rescue a species-poor, unproductive local community from the impacts of a novel predator. Naturally fishless alpine lake communities consisting of relatively large species were maladapted to, and therefore, suppressed by, introduced rainbow trout. Surprisingly, colonization by certain imported montane species not only negated, but later reversed the negative impacts of non-native trout on alpine communities. Analysis revealed that interspecific variation in body size best explained the interactive effects of the introduced invader and regional species pool on the local community. Below, I provide context and potential explanations for these key findings.

Although the regional species pool inocula significantly increased taxonomic richness across treatments (Fig. 3.1a), regional species failed to proliferate in the unstressed local communities and total zooplankton biomass increased only in the presence of fish (Fig. 3.1b). These results show that mass effects (i.e. high immigration rates) did not cause the biomass response. Rather, access to a regional species pool permitted the establishment of several fish-tolerant colonists, which functionally overcompensated for (i.e. more than offset) the loss of biomass incurred by suppression of the more sensitive alpine taxa (Fig. 3.2). These findings agree with the spatial insurance hypothesis that greater metacommunity diversity should impart resistance to stressed local communities via the supply of stress-tolerant individuals (Loreau et al. 2003); however, others have found mixed support. Here, possible confounding factors are differences in the nature of stressors (i.e. type and magnitude; Thompson & Shurin 2012, Symons & Arnott 2013) or dispersal treatments, which may introduce novel predators (Atobe et al. 2014) or tolerant species with poor resource-use efficiency (Matthiessen et al. 2010, Eggers et al. 2012). In comparison, I attribute increased invasion resistance by my dispersal treatment to both the severe initial impact of my invasion treatment, and the relatively high diversity and productive capacity of tolerant colonists in my regional species pool.

The unexpected net positive effect of the regional species pool and an invasive predator on zooplankton richness and biomass was likely caused by size-selective fish predation releasing smaller regional species from the influence of larger, dominant alpine taxa. For instance, large herbivores (e.g. *Daphnia* spp.) frequently monopolize food resources and competitively exclude smaller zooplankton species in the absence of visual predators (Gliwicz 1990). I found that fish stimulated algal production, creating a glut of resources available for consumers able to cope with the invader (Appendix B-4). The local community lacked such invasion-tolerant consumers, but aggregate community-level impacts were reversed by access to the regional species pool, which supplied several montane species likely already adapted to fish presence. This result shows how regional dispersal can mediate the local effects of biotic interactions (Cottenie & De Meester 2004, Howeth & Leibold 2010) and is consistent with other predator introductions that have increased prey diversity (e.g. Shurin 2001, Donald & Anderson 2003).

Spatial insurance effects require adequate propagule pressure to permit establishment of taxa from neighboring communities (Loreau et al. 2003). However, passive dispersal rates are difficult to measure and generally underestimated by colonization rates and population genetics (Bohonak & Jenkins 2003). For example, Allee effects (i.e. mate limitation and reduced population growth at low densities) may constrain colonization success by obligate sexual species (Kramer et al. 2008). Similar to the seeds of plants, crustacean zooplankton exhibit specific traits enabling long-distance passive overland dispersal (Bohonak & Jenkins 2003). For instance, cladocerans reproduce asexually to colonize novel habitats (Williamson & Reid 2010), and desiccation-resistant propagules (e.g. cladoceran ephippia and copepod diapause eggs) permit frequent transport by wind (Vanschoenwinkel et al. 2008) and waterfowl (via exterior attachment or passing through their digestive tracts; Proctor & Malone 1965, Frisch et al. 2007). In the context of stocked mountain lakes, zooplankton dispersal rates are uncertain and likely highly variable; however, attaching to boats of visiting anglers or flocks of migrating waterbirds could facilitate the movement of many migrants simultaneously. Although the dispersal treatment likely exceeded natural dispersal rates over the course of the experiment and thus accelerated the arrival of potential colonists, the recovery of certain stocked mountain lakes (e.g. Donald & Anderson 2003) suggests that regional migrants would eventually establish themselves and bestow a comparable, if delayed, rescue effect in invaded natural ecosystems. My results demonstrate the mechanistic potential for arriving species to mitigate local impacts of an invader, and underscore the conservation importance of maintaining regional biodiversity and connectivity in the face of global change.

While the biotic resistance hypothesis has mostly been related to community invasibility (Ricciardi et al. 2013), my results suggest that diverse communities are also more resistant against the impacts of invasion. I found that regional species pool inocula successfully increased the number of taxa in the zooplankton communities (Fig. 3.1a); however, the greater response diversity in the regional species pool also reflected the importance of species identity in driving biotic resistance. Specifically, the responses of individual taxa varied and aggregate community responses to invasion were driven by the losses and gains of a few dominant taxa (Fig. 3.2). The biomass contributions of most taxa changed very little with fish invasion, and those that responded positively (i.e. *Bosmina longirostris*, *Ceriodaphnia quadrangula*, and *Diacyclops thomasi*) were present only in the regional species pool (Fig. 3.2). Although the more diverse regional species pool contained greater resistance, my findings agreed with those of other studies in which community functioning (Lepš et al. 2001) and response to invasion (Daneshgar & Jose 2009) and species loss (Harvey et al. 2013) were mediated by the unequal contributions of certain dominant species (i.e. selection effects).

Significant trait–treatment associations suggest that differences in the invasion responses of individual taxa were related to variation in functional attributes. I found that smaller body sizes were associated with the fish invasion and regional species pool treatments using RLQ and fourth-corner analyses (Fig. 3.3; Table B-5.4). These associations linked community functional structure (i.e. abundance or productivity weighted distribution of species in functional trait space) with response to environmental change, and explained the reversal interaction between fish invasion and regional species pool treatments on community biomass. The smaller body sizes associated with taxa from the regional species pool permitted a positive response with fish presence, while the larger body sizes associated with taxa from the local species did not. Selection for small-bodied species in invaded communities indicates that prey community body size distribution may forecast the ecological impacts of invasion by planktivorous fish. Though the positive relationship between prey body size and vulnerability to visual aquatic predators is well established (Brooks & Dodson 1965), several additional traits potentially scale with body size (e.g. metabolism and dispersal ability) and others have noted the importance of this master trait for general ecosystem functioning and stressor resistance (e.g. Moore & Folt 1993, Hooper et al. 2005, Barnett et al. 2007, Ohlberger 2013, Boukal 2014).

Another factor thought to influence invasion impacts is environmental context, but contrary to my predictions, impacts were unaffected by higher temperatures. I had hypothesized that thermal stress would suppress larger stenothermic macrozooplankton, favouring smaller species that may also be less susceptible to fish predation. However, warming treatments had no significant effect on either zooplankton taxonomic richness or total biomass, and did not interact with invasion treatments (Fig. 3.1; Table 3.2). This was unexpected as biotic interactions involving fish are often sensitive to climatic variation (e.g. Gyllström et al. 2005, Hein et al. 2014, MacLennan et al. 2015). Though the warming treatment may have failed to generate significant effects because of its short duration or low magnitude of change, my results were similar to those of Jansson et al. (2010) who also found that fish presence exerted a much greater effect than temperature on cold-water lake zooplankton community structure.

Together, these findings point to metacommunity functional structure as a key determinant of the local and regional impacts of an invader. Though the relatively simple local alpine communities provided minimal resistance to invasion, my results show how importation of a regional species pool can dramatically alter the functional outcome of invasions by increasing response diversity. However, widespread invasions and other persisting regional stressors also increase the risk of biotic homogenization (Beisner et al. 2003) where diminished diversity may limit the resilience of native communities and their functional resistance to further environmental change (Olden et al. 2004). By assessing changes in community functional structure through links between stressor impacts and the prevalence of specific functional traits, biodiversity experiments can avoid restrictive interpretations of species-level sampling effects (i.e. greater likelihood of detecting tolerant species with increasing richness; Huston 1997) and reveal a stronger predictive understanding of community stressor response (Mouillot et al. 2013). My results demonstrate the use of RLQ and fourth-corner analyses as tools for exploring the magnitude and direction of impacts from invasive species and other ecological stressors.

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Chapter 4: Environmental and connectivity drivers of lake metacommunities along the North American Cordillera

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Note: a version of the chapter has been submitted for publication as Loewen CJG, Strecker AL, Larson GL, Vogel A, Fischer JM & Vinebrooke RD (2017).

Introduction

A long-standing challenge faced by ecologists and conservation biologists has been to unravel the multiple sources of variation affecting species composition of communities (Whittaker 1960, Jost et al. 2010, Anderson et al. 2011, Legendre & De Cáceres 2013). Here, covariance among environmental drivers can often confound ecological interpretations from observational studies, especially when data are spatially structured or evaluated over large geographic extents (Dray et al. 2006, Qian & Ricklefs 2012). Integration of species' response traits is also required, as they modify the effects of deterministic processes (e.g. environmental filtering and non-random dispersal) on species composition (Thompson & Townsend 2006, Farjalla et al. 2012). Identification of critical environmental and spatial structures, and the traits that mediate species' responses to these structures, is essential to filling knowledge gaps concerning how communities are assembled and respond to environmental changes (McGill et al. 2006, De Bie et al. 2012, Henriques-Silva et al. 2016, Loewen & Vinebrooke 2016).

The metacommunity concept (Leibold et al. 2004) provides a flexible framework for considering regional (e.g. atmospheric conditions, dispersal limitation) and local (e.g. abiotic tolerance, biotic interactions) drivers of species composition (e.g. Cottenie & De Meester 2004). Considerable interest exists in ranking the relative importance of assembly processes and their support for metacommunity paradigms (e.g. Cottenie 2005, Soininen 2016); however, there is also concern over restricting focus to specific typologies and objectionable space-for-dispersal assumptions (Anderson et al. 2011, Brown et al. 2017). To improve spatial interpretations, Monteiro et al. (2017) suggested that the dispersal limitation of communities be inferred from multispecies connectivity estimates, based on distances between occupied habitats. While there is a long precedent of evaluating spatial processes in metapopulations using patch connectivity (e.g. Moilanen 1999, Hanski & Singer 2001), this approach has only recently been applied to reveal dispersal limitation in natural metacommunities (Monteiro et al. 2017). Thorough investigation of the regional and local drivers of metacommunities also necessitates that the scale of inquiry be sufficiently broad to capture the amount of variation in environmental and spatial variables required for rigorous testing (Willig et al. 2003, Brown et al. 2017). For instance, Soininen (2016) pointed to studies conducted over large geographic scales as better highlighting the role of spatial structures (i.e. dispersal limitation); however, there have been few studies of metacommunity structure at even broader continental scales (e.g. Viana et al. 2016, Heino et al. 2017).

Lake communities are integrators of local catchment and atmospheric processes, positioning them well as sentinels of the multiple agents of global change (Jackson et al. 2016), especially in mountainous regions (Williamson et al. 2009). For instance, climate factors and terrestrial subsidies regulate energy and mass inputs to aquatic food webs, respectively (Juday 1940, Leavitt et al. 2009, Marcarelli et al. 2011). Freshwater communities are further influenced by terrestrial landscape characteristics (e.g. land cover, lithology, and topography), which mediate local hydrological and water quality conditions (Likens & Bormann 1974, D'Arcy & Carignan 1997, Hudson et al. 2003, Camarero et al. 2009), and invasive species, including globally introduced predatory salmonids (Crawford & Muir 2008, MacLennan et al. 2015). Mountain regions are also excellent venues for addressing biogeographical questions concerning species diversity because they inherently contain high levels of environmental heterogeneity (Lomolino 2001). Further, mountains are the source of headwaters and often exist in remote or protected areas, thereby offering unique opportunities for detecting subtle effects of regional drivers not blurred by the confounding impacts of more pronounced local perturbations (e.g. human land-use; Kollmair et al. 2005).

I examined zooplankton beta diversity patterns (defined here as variance in species composition; Legendre & De Cáceres 2013) across the North American Cordillera to infer the relative importance of community assembly processes and generate hypotheses of how these communities respond to environmental change. Zooplankton are useful model organisms in ecology and biogeography because they disperse widely, have central roles in aquatic food webs, and reproduce rapidly – making them responsive to environmental variation (Lampert 2006). Given the vast geographic scale of my investigation (spanning nearly 30° of latitude), I expected that spatially structured environmental filters would explain a large proportion of total species variance. For instance, I predicted that strong regional climate signals would covary with space and climate-sensitive land cover types (e.g. forested areas and wetlands). A functional approach was also used to uncover deterministic links among species' traits and environmental and spatial constraints. Here, I hypothesized that occurrence of smaller species better adapted metabolically to thermal variation (Moore et al. 1993) and avoidance of size-selective predation (Brooks & Dodson 1965, Loewen & Vinebrooke 2016) would be less related to lake temperature and the presence of invasive fish, respectively. Finally, if dispersal limitation is trait-based, then the spatial configuration of suitable habitats should impose non-random species selection (Edelaar & Bolnick 2012). Thus, I also predicted stronger spatial patterning of obligate sexual than cyclically parthenogenetic asexual species due to suspected Allee effects (i.e. mate limitation; Kramer et al. 2008), as overland dispersal by zooplankton is passive and potential topographic barriers to dispersal are common in mountain regions.

Materials and methods

Study area and zooplankton data

Crustacean zooplankton communities were assessed for 1,234 mountain lakes and ponds along the North American Cordillera, from the Mackenzie Mountains in the Yukon Territory to the Sierra Nevada in California, USA (Fig. 4.1). The geographic positions of sampling locations spanned large, continental-scale latitudinal (29.6° or 3,292 km), longitudinal (17.7° or 1,585 km), and elevation (3,741 m asl) gradients. Historical data were obtained following an extensive review of available literature. Data sources included 30 published articles, 32 government reports, and results from previously unpublished surveys (see Appendix C-1 for full list of references). Unpublished results include internal reports communicated by government scientists (Environment Canada, National Park Service, and United States Forest Service) and supplementary records from past surveys. Data for each site are cumulative records of all species occurrences. Most samples had been collected over the past 50 years (Fig. 4.2). Although sampling effort varied among locations (1–11 years), samples were generally collected following a standard protocol for evaluating pelagic zooplankton communities during the open-water season (May–September). Zooplankton were collected by pulling conical nets (mesh-size of 250 μm or smaller) through the water column, either vertically from near the center of the lake or horizontally from the shore, depending on depth. Samples were preserved with ethanol or dilute formalin solution and later enumerated by stereoscopic microscopy.

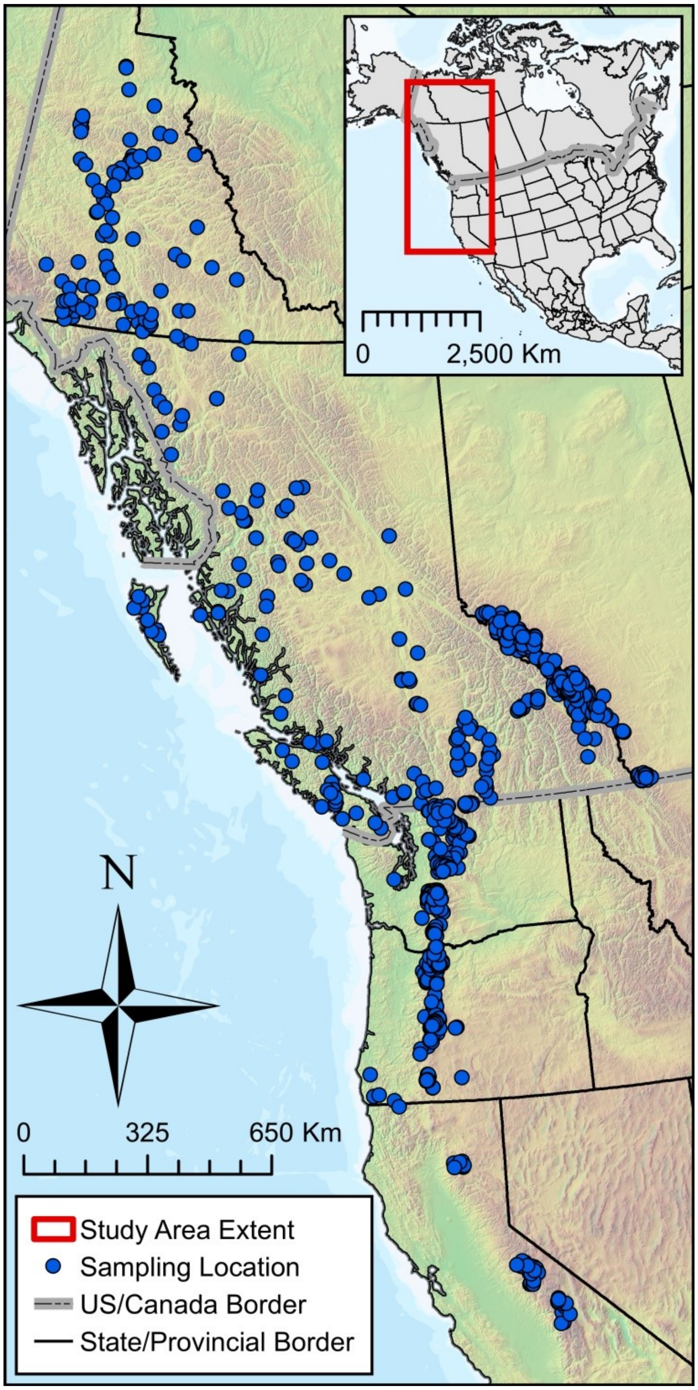

Fig. 4.1 Surface water sampling locations across the North American Cordillera. Shaded relief imagery developed by Esri. Map projection is custom complex Transverse Mercator.

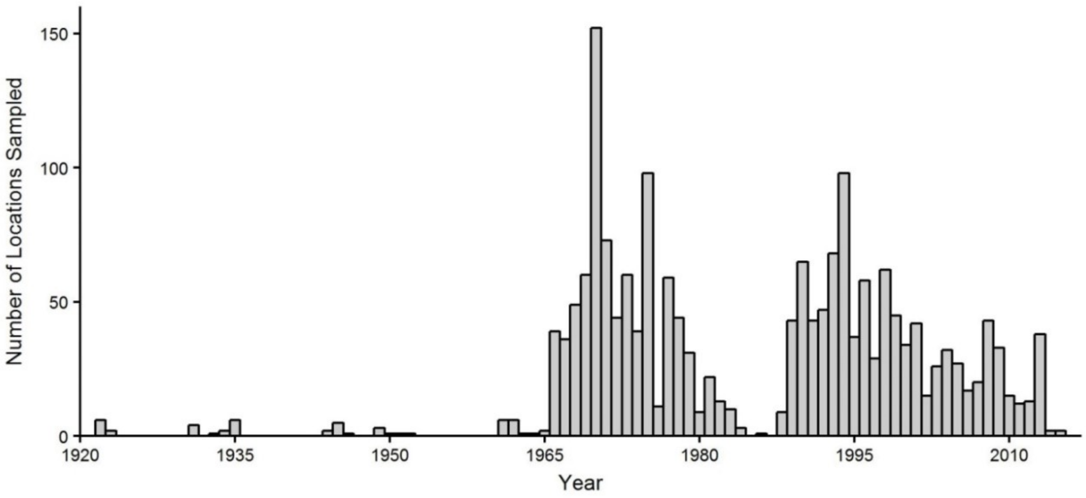

Fig. 4.2 Distribution of zooplankton sampling events. Counts are the number of locations sampled each year (1922–2015). Counts do not indicate duplicate samples collected within a single year. Exact sampling dates were uncertain in some instances and several were inferred from associated water quality monitoring programs.

Species-level records were standardized to follow taxonomy established by Edmondson (1959), with updates. Species occurring in fewer than 5% of sites were excluded from analyses because records of rare species were deemed less reliable and also contribute less to turnover than common species in aquatic metacommunities (Heino & Soininen 2010). Records for certain potentially hybridizing or otherwise difficult to distinguish species were combined to improve consistency: *Daphnia pulicaria* was merged with *Daphnia pulex*, *Diaphanosoma brachyurum* was merged with *Diaphanosoma birgei*, *Diacyclops bicuspidatus thomasi* was merged with *Diacyclops thomasi*, and *Daphnia galeata mendotae* and *Daphnia mendotae* were merged with *Daphnia galeata*. Only species-level identifications were considered. Twenty-nine species were evaluated and assigned categorical traits based on their reproductive biology and body size (Table 4.1). Reproductive categories represent a major functional division between cyclically parthenogenetic asexual cladoceran and oblitate sexual copepod zooplankton. Body sizes classifications (small or large) were based on a natural break in the distribution of body lengths, at 1.37 mm. Historical body length measurements (MacLennan et al. 2015, Loewen & Vinebrooke 2016) were supplemented with records compiled by Hébert et al. (2016). For some species where body length measurements were unavailable, length estimates were taken from a similar member of the same genus.

Table 4.1 Zooplankton functional trait classifications and estimated body lengths (mm).

Traits	Asexual	Sexual
Small	*Chydorus sphaericus* (0.32)	*Microcyclops varicans* (0.59)
	Alona guttata (0.35)	*Diacyclops thomasi* (0.92)
	Bosmina coregoni (0.40)	*Leptodiaptomus angustilobus* (1.05)
	Bosmina longirostris (0.40)	*Leptodiaptomus signicauda* (1.05)
	Ceriodaphnia quadrangula (0.55)	*Eucyclops agilis* (1.10)
	Diaphanosoma birgei (0.61)	*Acanthocyclops vernalis* (1.20)
	Holopedium gibberum (0.77)	*Leptodiaptomus tyrrelli* (1.24)
	Polyphemus pediculus (0.83)	
	Daphnia longiremis (0.84)	
	Daphnia dentifera (1.17)	
Large	*Daphnia galeata* (1.50)	*Cyclops scutifer* (1.50)
	Daphnia pulex (1.75)	*Epischura nevadensis* (1.75)
	Daphnia schödleri (1.93)	*Aglaodiaptomus leptopus* (2.00)
	Daphnia middendorffiana (2.00)	*Macrocyclops albidus* (2.00)
		Hesperodiaptomus arcticus (2.50)
		Hesperodiaptomus franciscanus (2.50)
		Hesperodiaptomus kenai (2.50)
		Hesperodiaptomus shoshone (2.50)

Environmental variables

Sets of environmental predictors, including climate (mean annual air temperature, total annual precipitation, and mean incoming solar radiation), catchment/lake conditions (morphometry, land cover, and lithology), and introduced fish status (present/absent), were estimated at each sampling location (Table 4.2). Climate and catchment/lake variables were derived using ArcGIS for Desktop (Esri 2016). Variables were natural log-transformed to increase linearity where doing so improved model fit, and standardized (i.e. centered and scaled) to account for differing measurement units. Fish introduction status was estimated at each waterbody following a review of historical salmonid stocking and occurrence records (see Appendix C-2 for full bibliography). A potential for zooplankton communities to be affected by introduced fish was assumed where records indicated recent stocking efforts or presence of exotic species prior to sampling.

Waterbodies were assumed to have not been stocked in the absence of such historical accounts. Fish introduction status was treated as a binary variable (present or absent).

Table 4.2 Summary statistics for environmental parameters.

Parameter	Min	Max	Mean	Median	SD
Climate					
Annual Mean Air Temperature (K)	264	284	275	275	3
Annual Total Precipitation (mm)	253	3,375	1,173	770	761
Mean Solar Radiation (WH/m^2)	528,484	1,191,327	859,434	882,191	108,794
Catchment/Lake – Land Cover (proportion)					
Agricultural	0	0.0050	0.000005	0	0.0001
Barren Land	0	1.0000	0.2191	0.0598	0.2857
Developed (Non–Vegetated)	0	0.2655	0.0019	0	0.0133
Forest (Coniferous)	0	1.0000	0.4756	0.4967	0.3525
Forest (Deciduous)	0	0.7866	0.0146	0	0.0466
Forest (Mixedwood)	0	0.2615	0.0047	0	0.0193
Grassland/Herbaceous	0	0.9192	0.0770	0.0302	0.1199
Perennial Ice/Snow	0	1.0000	0.0227	0	0.0761
Shrub/Scrubland	0	1.0000	0.1235	0.0742	0.1464
Surface Water	0	0.4884	0.0506	0.0318	0.0618
Wetlands (Emergent/Herbaceous)	0	0.4286	0.0045	0	0.0243
Wetlands (Wooded/Shrub)	0	0.6000	0.0058	0	0.0291
Catchment/Lake – Lithology (proportion)					
Acidic Plutonics	0	1.0000	0.1349	0	0.3086
Acidic Volcanics	0	0.9490	0.0053	0	0.0530
Carbonate Sedimentary Rock	0	1.0000	0.0220	0	0.1173
Evaporite	0	0.0028	0.000003	0	0.00009
Metamorphic Rock	0	1.0000	0.0558	0	0.2025
Mixed Sedimentary Rock	0	1.0000	0.2847	0	0.4294
Non–Acidic Plutonics	0	1.0000	0.0117	0	0.0807
Non–Acidic Volcanics	0	1.0000	0.3167	0	0.4330
Non–Carbonate Sedimentary Rock	0	1.0000	0.1261	0	0.2911
Pyroclastics	0	0.7063	0.0019	0	0.0253
Unconsolidated Sediment	0	1.0000	0.0408	0	0.1435
Catchment/Lake – Morphometry					
Catchment Area (m^2)	3,469	46,543,543,866	216,487,160	1,490,667	1,852,186,244
Catchment Aspect (°)	3	322	169	170	48
Catchment Slope (°)	0.0002	40.6467	16.5434	16.5366	9.1297
Lake Area (m^2)	95	592,000,943	5,141,734	47,264	35,008,039
Lake Perimeter (m)	43	680,290	8,708	974	38,689
Fish Introduction (present/absent)	0	1	0.49	0	0.50

Watershed delineation and subsequent geoprocessing were based on one arc-second (<30 m) resolution digital elevation maps (DEMs) from the National Elevation Dataset (U. S. Geological Survey 2016a), and the locations of 1:24,000 scale hydrological features from the National Hydrography Dataset (U.S. Geological Survey 2016b) and the National Hydrology Network (Natural Resources Canada 2004). Geographic coordinates for sampling locations were spatially joined with waterbody polygons and confirmed/corrected using satellite imagery (Esri 2016). Study areas were projected and analyzed using standard state plane or regional projections to minimize local measurement error.

Terrain preprocessing and watershed delineation procedures were adapted from Esri (2013) for dendritic drainages. DEM manipulation involved filling all sinks to resolve erroneous pits and ensure continuous flow through each hydrological system. DEMs were then reconditioned to emphasize known drainage networks by burning a 10 m trench along stream polylines (AGREE method; Hellweger 1997). Because DEMs lacked bathymetry information, lake polygons were levelled and dropped by 10 m to improve consistency around their perimeters. I then filled any new sinks in the DEMs (created during reconditioning or levelling procedures) and delineated watersheds for each lake polygon from estimated flow direction grids.

Catchment and lake boundaries were used to overlay grids of relevant climate and landscape attributes and calculate zonal summaries for each sampling location. Mean catchment aspect, mean catchment slope, and minimum lake elevation were estimated from unprocessed DEMs. Catchment and lake sizes were calculated directly from their feature layers. Fifty year-mean annual total precipitation at each catchment and annual mean air temperature at each lake surface (1950–2000) were calculated from 30 arc-second (~1 km) grids interpolated from monthly climate records (Hijmans et al. 2005, Commission for Environmental Cooperation 2011). Mean incoming solar radiation was estimated at each waterbody using the Area Solar Radiation tool (Esri 2016). Direct and diffuse insolation (WH/m^2) was calculated over an 18 week period (May 20–September 23), approximating the open-water season in North American mountain lakes. Calculations were based on geographic positions (latitude and elevation), proximal topography (i.e. shadow cover), and atmospheric conditions (i.e. cloud cover). Waterbody elevations and 20 km upward-looking viewsheds (512 x 512 cells) were estimated from unprocessed DEMs. Mean latitude and cloud cover (1950–2000; University of East Anglia Climatic Research Unit 2012) were estimated individually for groups of waterbodies occupying cells on a 0.5 degree grid. Cloud cover estimates were used to calculate transmittivity (*t*) as:

$$t = (0.7 \times P_{clear}) + \left(0.3 \times P_{cloudy}\right)$$

and diffuse proportion (*d*) as:

$$d = (0.2 \times P_{clear}) + (0.7 \times P_{cloudy})$$

where P_{clear} and P_{cloudy} were the estimated proportions of clear and cloudy days, respectively (adapted from Huang et al. 2008). The standard overcast model was used to estimate diffuse radiation (i.e. incoming flux varied with zenith angle). Viewshed calculations used 64 azimuth directions to capture complex topography.

Land cover characteristics at each catchment were calculated from one arc-second (<30 m) resolution grids derived by the Earth Observation for Sustainable Development of Forests (2006) project and the National Land Cover Database (U.S. Geological Survey 2014) from various Landsat imagery and ancillary data (circa 2000–2001). The data were merged and reclassified to 12 cover classes, including: surface water, perennial ice/snow, developed (non-vegetated), barren land (rock/sand/clay), coniferous/evergreen forest, deciduous/broadleaf forest, mixedwood forest, shrub/scrubland, grassland/herbaceous, agricultural (cropland/pasture), wooded/shrub wetland, and emergent/herbaceous wetland. Undefined areas (including cloud cover and shadows) were subtracted from the total catchment area before calculating the proportional representation of each land cover class.

Catchment lithology was calculated from 7.5 arc-second (<250 m) resolution grids assembled for the Global Ecological Land Unit Map (Sayre et al. 2014). Lithology classes included acidic plutonics, acidic volcanics, carbonate sedimentary rock, evaporite, metamorphic rock, mixed sedimentary rock, non-acidic plutonics, non-acidic volcanics, non-carbonate sedimentary rock, pyroclastics, and unconsolidated sediment. As with land cover estimates, undefined areas were subtracted from the total catchment area before calculating the proportional representation of each lithology class.

Spatial variables

Sets of spatial predictors, including geographic positions, spatial autocorrelation (space), and patch connectivity, were estimated at each sampling location. Geographic positions included the latitude, longitude, and elevation of each waterbody. Positive spatial autocorrelation (space) was modelled using distance-based Moran's eigenvector maps (dbMEMs), which were derived from a matrix of minimum planar distances between lake polygons, truncated by the largest distance in a minimum spanning tree (290,189 m; Dray 2006, Dray et al. 2017). Tests using larger truncation thresholds did not improve model fit (results not shown). Distances were estimated using a custom Transverse Mercator projection centered over the study area.

Dispersal limitation was inferred from patch connectivity using methods and code from Monteiro et al. 2017. Connectivity was modeled using two multispecies metrics, distance to nearest occupied lake and average connectivity (Hanski & Singer 2001), computed by combining single species estimates. Average connectivity was calculated as:

$$c_{ik} = \sum_{\substack{i=1 \\ i \neq j}}^{n} o_{jk} \exp(-\frac{d_{ij}}{\alpha})$$

where *c* is the connectivity value for the *k*th species at lake *i*, *o* is the occupancy state (present = 1 or absent = 0) of species *k* at lake *j*, *d* is the minimum planar distance between lake polygons *i* and *j*, and α is a constant controlling the exponential dispersal kernel (Monteiro et al. 2017). As zooplankton dispersal rates are poorly understood, especially at large scales, an iterative procedure was used to select single α values for the overall community and each functional group that maximized species variance explained by *c* (Monteiro et al. 2017). I tested 100 values of α between the minimum (1 m) and maximum (3,482,204 m) distances between lake polygons.

Statistical analyses

Variation in species composition linked to environmental and spatial predictors was assessed by transformation-based redundancy analysis (tbRDA) and variation partitioning of Hellinger-transformed species presence-absence data (Peres-Neto et al. 2006, Legendre & De Cáceres 2013, Monteiro et al. 2017). Hellinger pre-transformation on presence-absence data preserves Ochiai distances, which are metric, and is appropriate for canonical variation partitioning

(Legendre & De Cáceres 2013, Monteiro et al. 2017). Parsimonious environmental and spatial autocorrelation models were obtained by partial tbRDA and automatic forward stepwise selection, using permutation tests (with 100,000 residual iterations) to find statistically significant explanatory variables that maximized explained variance (i.e. adjusted R^2; Blanchet et al. 2008, Oksanen et al. 2017). Forward selection was also applied to obtain optimal climate and catchment/lake predictor sets (see Table C-3.1 in Appendix C-3 for final environmental models).

Following model selection, fractions of variation linked to environmental and spatial predictors were evaluated by variation partitioning analyses. First, the relative importance of environment was compared against the space and geographic predictor sets (Model 1). I then probed the environmental component, evaluating variation attributable to specific sets of environmental predictors (climate, catchment/lake, and introduced fish) while controlling for the effects of space (Model 2). The total and unique fractions of variation attributable to individual environmental predictors (e.g. solar radiation and separate land cover classes) were also estimated, treating the full forward selected environmental model and space as covariables (Model 3). Finally, I assessed the spatial component of variation in greater detail, comparing spatial autocorrelation (space), patch connectivity, and environmental components (Model 4). Analyses were repeated for each reproductive (sexual vs. asexual) and body size (small vs. large) group to evaluate the role of traits in mediating species' response to environmental and spatial structures.

All analyses were conducted using R (R Core Team 2016). Hellinger transformation, model selection, redundancy analysis, and variation partitioning analysis were conducted using the 'decostand', 'ordi2step', 'rda', and 'varpart' functions in the 'vegan' package (Oksanen et al. 2017). Distance-based Moran's eigvenvector maps were computed using the 'dbmem' function in the 'adespatial' package (Dray et al. 2017). Explanatory connectivity matrices were computed using methods and code from Monteiro et al. 2017. A Fisher's exact test was conducted using the base R function (R Core Team 2016) to confirm that the traits were orthogonal ($P = 0.26$).

As this study is a quantitative synthesis of multiple historical data sources, there exists potential for my results to reflect biases among individual sampling locations or studies. To evaluate the extent to which my interpretations may be confounded by variations in sampling effort, sampling year, or data source (i.e. research group or taxonomist), I conducted a series of sensitivity analyses. Results of these analyses indicate that my findings are robust and support the following interpretations (see Appendix C-4 for details).

Results

Environment and space best explained variance in species composition (Model 1), describing 22.86 and 24.73% of total variance, respectively (Fig. 4.3a). Geography explained 15.87 % of total species variance; however, only 0.28 % of variation was uniquely attributed to geographic position (compared to 3.24 and 5.40 % for environment and space, respectively). The majority of species variance linked to geography also covaried with environment and space (12.81 %; Fig 4.3a). These results showed that species variance along the geographic scale of the investigation was largely captured by the environmental and spatial autocorrelation predictors considered, though each total and unique fraction of species variance was significant (Table C-3.2).

The predictive variables better explained variance among obligate sexual (copepod) and large species than asexual (cladoceran) and small species (Fig. 4.3b). For instance, space uniquely explained 7.15 and 8.21 % of species variance for sexual and large species, respectively, compared to 4.66 and 4.40 % of variance for asexual and small species. Similarly, environmental variables uniquely captured 4.27 and 2.95 % of species variance for large- and small-bodied species, respectively, though variance attributable to environment was similar among sexual and asexual species (3.17 and 3.53 %, respectively). Otherwise, the ranked importance of explanatory matrices was the same across all trait groups (i.e. space > environment > geography; Fig. 4.3b) and all testable fractions of species variance in Model 1 were significant (Table C-3.2).

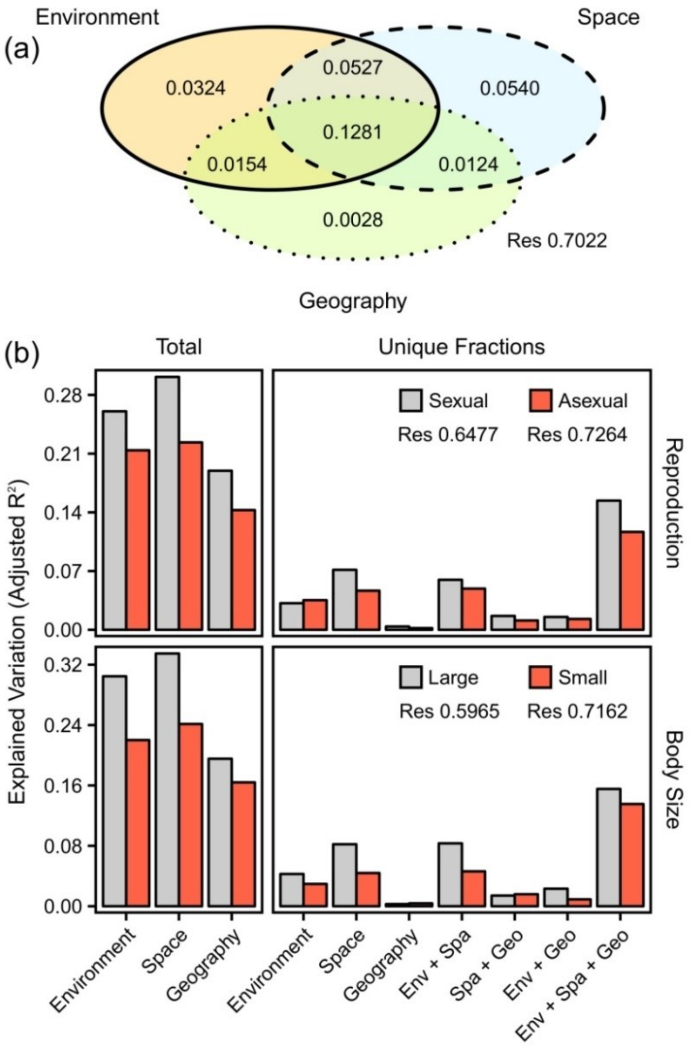

Fig. 4.3 (Model 1) Total, unique, and shared proportions of variance in species composition (adjusted R^2) attributable to environment (Env), space (Spa), and geography (Geo) predictor sets for the (a) overall community (*n* = 1,234) and (b) species trait groups (*n* = 1,155, 1,103, 1,014, and 1,142 for sexual, asexual, large, and small species, respectively). Res refers to model residuals.

Analysis of environmental predictor sets when controlling for spatial autocorrelation (Model 2), showed that variance in species composition was more influenced by local catchment/lake features than climate or fish introduction (Fig. 4.4a). Each environmental predictor set was significant, but most variance was linked to space (Table C-3.3). For instance, covariance among climate, catchment/lake features, and space accounted for the largest fraction of explained variation, both overall (Fig. 4.4a) and across trait groups (Fig. 4.4b). Although fish introduction explained relatively little variation compared to the multi-parameter catchment/lake and climate predictor sets (Fig. 4.4), fish were of greater importance in the context of unique variance linked to individual environmental parameters (see Model 3; Fig. 4.5).

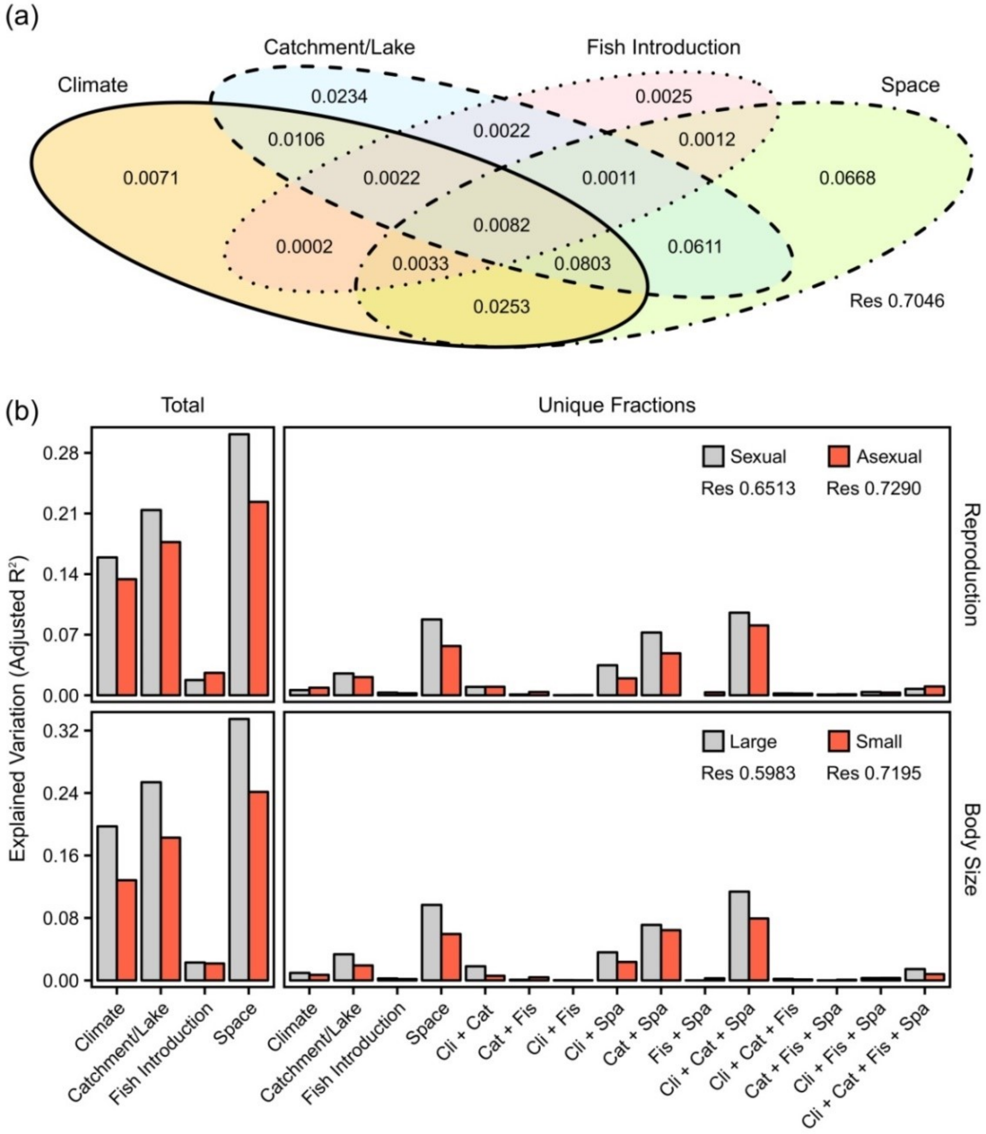

Fig. 4.4 (Model 2) Total, unique, and shared proportions of variance in species composition (adjusted R^2) attributable to climate (Cli), catchment/lake (Cat), fish introduction (Fis), and space (Spa) predictor sets for the (a) overall community (*n* = 1,234) and (b) species trait groups (*n* = 1,155, 1,103, 1,014, and 1,142 for sexual, asexual, large, and small species, respectively). Res refers to model residuals.

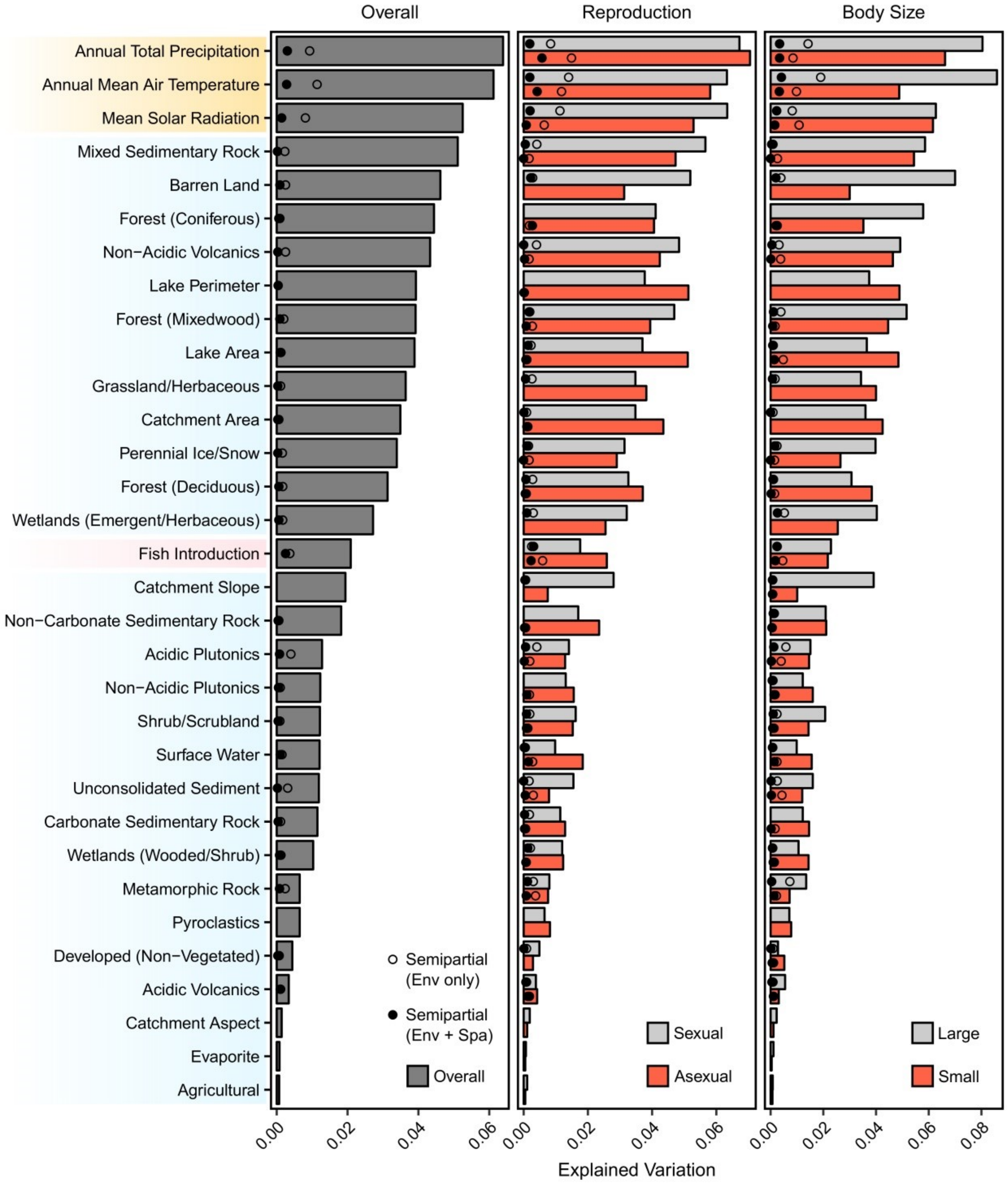

Fig. 4.5 (Model 3) Total and unique proportions of variance in species composition (adjusted R^2) attributable to individual environmental variables for the overall community (*n* = 1,234) and species trait groups (*n* = 1,155, 1,103, 1,014, and 1,142 for sexual, asexual, large, and small species, respectively). Unique species variance estimates are semipartials (conditioned by other environmental [Env] parameters and space [Spa]). Orange shaded variables are climate (Cat) parameters, blue shaded variables are catchment/lake (Cli) parameters, and the pink shaded variable is fish status (Fis).

Climatic factors were the most important environmental variables individually (Model 3); however, the relative ranking of parameters varied based on functional traits (Fig. 4.5). For instance, air temperature and precipitation explained more variance among large species, while lake area was of greater importance to smaller species (Fig. 4.5). Environmental associations also varied based on reproductive biology as obligate sexual copepods had stronger links to barren lands than asexual cladocerans, which were generally more associated with forested areas (Fig. 4.5). Total variance attributable to introduced fish was of intermediate importance; however, fish effects were generally less spatially autocorrelated than other predictors and thus variance uniquely linked to fish was relatively large and exceeded that of ang single catchment/lake variable (Fig. 4.5). Fish effects also varied between trait groups as total and unique species variance (controlling for both environmental and spatial parameters) were marginally greater for larger species (Fig. 4.5). Total variance linked to fish was also greater for asexual species; however, fish effects were more spatially autocorrelated for asexual species, making their interpretation less certain (Fig. 4.5). Total fractions of species variance were significant for nearly all individual environmental parameters (except evaporate lithology for small species); however, unique variance partitions conditioning for space were insignificant for several land cover and lithology types (Table C-3.1).

Connectivity explained less total species variance (16.99%) than the environment and space predictor sets (Model 4; Fig. 4.6a). Connectivity and space, which were both based on distances between lake polygons, covaried among themselves and with environment (Fig. 4.6a). Species variance uniquely attributable to connectivity was relatively low (0.57 %), but significant (Table C-3.4). The fractions of variance attributed to potential dispersal limitation (i.e. unique variation attributable to connectivity in addition to that shared with space) were greatest for obligate sexual and large species (Fig. 4.6b).

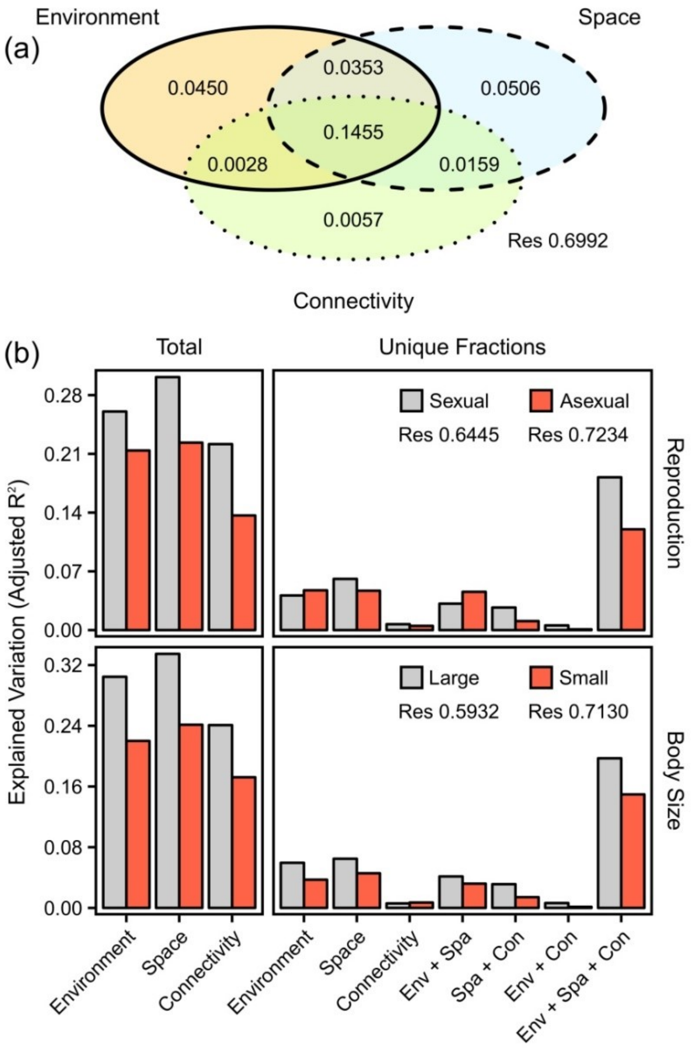

Fig. 4.6 (Model 4) Total, unique, and shared proportions of variance in species composition (adjusted R^2) attributable to environment (Env), space (Spa), and connectivity (Con) predictor sets for the (a) overall community (*n* = 1,234) and (b) species trait groups (*n* = 1,155, 1,103, 1,014, and 1,142 for sexual, asexual, large, and small species, respectively). Res refers to model residuals.

Discussion

I found that zooplankton beta diversity across the North American Cordillera was explained by multiple covarying local and regional drivers, and mediated by species' functional traits. Climate, catchment/lake, and spatial components of the geographic factor (i.e. autocorrelation) best explained variance in species composition (Fig. 4.4), supporting biogeographic theories that relate spatial variation and geographic gradients to the origin and maintenance of species diversity patterns (e.g. Lomolino 2001, Willig et al. 2003). Local catchment/lake features were the most important set of environmental predictors (Fig. 4.4); however, the relative importance of single parameters varied by trait, and climate and fish introduction generally captured the most unique variation individually (Fig. 4.5). Species variance showed a large amount of spatial structure, but because processes other than dispersal can cause spatial autocorrelation, I used a multispecies patch connectivity framework to infer dispersal dynamics (Monteiro et al. 2017). I found that patch connectivity was more important for larger, sexual (copepod) species, but this broader regional factor explained less variation than local environmental constraints (Fig. 4.6). Together, my findings highlight the hierarchical importance of local and regional factors of metacommunity assembly in mountain lakes, and provide insight into how communities may respond to future environmental changes.

The broad geographic gradients covered by my study enabled a unique perspective on biodiversity patterns in relation to environmental variation. Climate factors and several catchment/lake features (e.g. lithology and climate-mediated land cover types) were spatially structured and covaried with geographic position (Fig. 4.3). However, the limited influence of geography relative to environment (in terms of uniquely explained variation; Fig. 4.3) provided evidence for determinism in the system, as neutral theory predicts that community dissimilarity should primarily increase with distance (Willig et al. 2003). Rather than constituting opposing viewpoints, though, random and non-random processes may jointly influence community composition with varying effects on species mediated by functional traits (Thompson & Townsend 2006). For instance, I found that both total and unique variation attributable to environment were greater for larger species (Fig. 4.3), a finding that agreed with Farjalla et al. (2012), who proposed that determinism increases with organism size. My results also suggested that determinism is greater for sexual species, perhaps because limited dispersal (and thus potential to generate rescue or mass effects) reduces their occurrence under less favourable conditions.

The lead ranking of catchment/lake features across functional trait groups (Fig. 4.4) highlights the importance of terrestrial–aquatic linkages. Terrestrial influences on aquatic ecosystems include direct energy and mass subsidies (Juday 1940, Leavitt et al. 2009, Marcarelli et al. 2011) in addition to indirect effects of catchment morphometry, lithology, and land cover on local hydrological and water quality conditions (e.g. D'Arcy & Carignan 1997, Camarero et al. 2009). Here, catchment morphometry (particularly slope) dictates local water residence time and overland flow rates, as well as the transport of various dissolved and particulate substances (including carbon, phosphorous, and nitrogen; Likens & Bormann 1974, D'Arcy & Carignan 1997). Similarly, groundwater inputs to mountain lakes are affected by catchment lithology, which influences their conductivity, alkalinity, and concentrations of heavy metals (Marchetto et al.1995, Füreder et al. 2006, Camarero et al. 2009). For instance, weathering of highly soluble carbonate rocks is a major contributor to elevated pH and total alkalinity in alpine waters (Camarero et al. 2009). Allochthonous (i.e. terrestrially-derived) inputs, which vary with land cover, subsidize aquatic food webs and further alter water chemistry (Likens & Bormann 1974). Human-impacted land cover types (e.g. agricultural and urbanized lands), which are of critical relevance globally (Carpenter et al. 1998), had little influence on community variation in my study because mountain headwaters are largely undeveloped and most are in protected areas (Kollmair et al. 2005). While topography and surficial geological conditions are inherently stable, land cover types such as forests, wetlands, and perennial snow and ice (i.e. glaciers) are relatively sensitive to environmental changes. For example, glaciers are projected to decrease by 90% by 2100 in the Canadian Rocky Mountains (Clark et al. 2015), and to disappear in the USA by 2030 (Hall & Fagre 2003). Aquatic habitat coupling with these sensitive land cover types is critical, as their influence on the loading of suspended sediments and dissolved nutrients into freshwater ecosystems will have implications for future water quality and productivity (D'Arcy & Carignan 1997, England & Rosemond 2004, Vinebrooke et al. 2010).

My results also suggest that climate has a critical role in species sorting along geographic gradients, as precipitation, temperature, and solar radiation parameters explained the most variation in overall community composition individually (Fig. 4.5). These results support previous studies, which have shown that larger species are more affected by temperature (Moore et al. 1993), and that solar radiation is a major factor of diversity patterns in temperate lakes (Pinel-Alloul et al. 2013, Lyons & Vinebrooke 2016). However, the chief importance of total annual precipitation regimes in driving planktonic community composition across mountain lakes is less recognized (but see phytoplankton response from Parker et al. 2008). Precipitation can affect lake alkalinity and inputs of heavy metals, dissolved organic carbon, and turbidity, influencing water clarity and productivity (e.g. Hudson et al. 2003), but the most obvious effect of precipitation is influence on local hydrology. Across the study region, lakes received the most precipitation during winter months (November–February; data not shown), when precipitation falls as snow. The total volume of accumulated winter snowpack subsequently dictates critical spring-time hydrological conditions. For instance, low winter snow accumulation may lead to reduced water levels or desiccation in smaller temporary ponds, while high rates of runoff from large snowpack may disrupt pelagic biota in mountain lakes (Girdner & Larson 1995). Even in remote regions, meltwater can provide ion pulses or deposit persistent pollutants accumulated over winter snowpack (Carrera et al. 2001). The relatively large proportions of species variance attributable to temperature, solar radiation, and precipitation highlight the vulnerability of mountain zooplankton communities to climate change, which may be compounded by climate-mediated changes to other environmental variables, such as land cover alterations or enhanced predation rates by exotic fishes (Messner et al. 2013, Symons & Shurin 2016).

Salmonid introductions have impacted freshwater ecosystems globally (Crawford & Muir 2008). In western North America, stocking programs have spread native fish species (e.g. *Oncorhynchus clarkii* and *O. mykiss*) outside of their historical ranges and introduced exotic species that had previously not occurred (e.g. *Salvelinus fontinalis* and *Salmo trutta*) – often into historically fishless lakes where native biota were maladapted to the alien predators (Knapp et al.2001). I found that fish introductions exerted a relatively large unique effect on zooplankton composition, which varied based on species' functional traits (Fig. 4.4). However, the total variance explained by fish introduction was less than anticipated, possibly because their effects were confounded by differences between stocking programs (e.g. species or density stocked), the overlapping distributions of native fishes, or environmental context (e.g. Messner et al., 2013). As predicted from previous studies (e.g. Brooks & Dodson 1965, Loewen & Vinebrooke 2016), variation attributable to the introduced predators was size-selective and marginally greater for large species (Fig. 4.4b). Further, I found evidence that fish effects were stronger for asexual (cladoceran) species; however, this result is uncertain because species variance was confounded by spatial autocorrelation (Fig. 4.4b). A possible explanation for a greater influence of fish on asexual zooplankton is differences in swimming behavior and predatory escape response. For instance, *Daphnia* spp. (which are cyclically parthenogenic) are conspicuous to visual planktivores and more easily captured than obligate sexual (copepod) species (Hutchinson 1967, Drenner et al. 1978). My results demonstrate the historical legacy of fish stocking in North America and, controlling for confounding local and regional factors, highlight the general sensitivity of freshwater communities to invasive predators.

Zooplankton can passively disperse between isolated lake habitats by wind or animal vectors. For instance, desiccation-resistant propagules can attach to the exterior of passing organisms (including migrating waterfowl or human anglers) and survive long-distance transport in bird digestive tracts (Green & Figuerola 2005). Because zooplankton dispersal rates are challenging to measure directly, ecologists often infer dispersal dynamics from species' spatial distributions. I estimated community dispersal limitation using multispecies patch connectivity estimates derived from common metapopulation metrics (Monteiro et al. 2017). This novel approach permits evaluation of dispersal patterns without space-for-dispersal substitution, a frequent assumption that has been contested because patterns of spatial autocorrelation may be confounded by unmeasured environmental variables, which are themselves spatially structured (Anderson et al. 2011, Brown et al. 2017, Monteiro et al. 2017). I found that connectivity covaried strongly with space, since both predictors were based on distances between lakes; however, connectivity explained less variance in species composition (Fig. 4.6). I also found that connectivity explained less variation than environment (Fig. 4.6), suggesting that species sorting along environmental gradients may be more important than dispersal limitation in mountain zooplankton communities. Still, I found that a considerable amount of spatial autocorrelation remained unaccounted for by environment and connectivity predictors (Fig. 4.6), pointing to the existence of other unmeasured sources of spatial variation. I also discovered that variation attributable to connectivity was greatest for large and obligate sexual species (Fig. 4.6b). These findings show that zooplankton dispersal is non-random, and support past studies that have identified size-selective passive dispersal limitation (e.g. van de Meutter et al. 2008, De Bie et al. 2012) and the potential for Allee effects to constrain colonization by obligate sexual copepods (Kramer et al. 2008).

While my results are correlative, and thus cannot provide causal evidence of community assembly or species' response to environmental constraints, the patterns observed in my study generate several interesting hypotheses. For instance, the prevalence of trait-based variation in response to environmental and spatial structures highlights the importance of deterministic processes driving zooplankton community composition. The role of climate factors, in addition to other climate-sensitive catchment attributes (e.g. barren, forest, wetland, and perennial ice/snow land covers), underscores the sensitivity of mountain lake communities to climate change. In particular, the discovered significance of annual precipitation suggests that changes to rain/snow regimes may exert considerable influence on communities by altering their local hydrological and/or water quality conditions. Conversely, several important environmental variables are inherently constant (e.g. lithology and catchment morphology) and thus may act to stabilize communities in times of change.

To my knowledge, this study is the largest and most comprehensive assessment of freshwater zooplankton beta diversity to date – and the first to organize the trait-based hierarchical importance of climate, terrestrial–aquatic habitat coupling, invasive species, and patch connectivity on metacommunity structure at a continental scale. Thus, my findings offer insights into the potential impacts of increasingly rapid environmental changes on aquatic biodiversity and their functional consequences across a broad range of lakes. For instance, larger species were more influenced by temperature and fish introduction, suggesting they may be sensitive to climate warming and biological invasions. Larger and sexual (copepod) species were also the most structured by patch connectivity, highlighting how they may have limited potential to track changing environmental conditions. In contrast, variation in smaller and asexual (cladoceran) species were less structured by temperature and connectivity, reflecting perhaps their greater dispersal ability and potential for rescue effects on stressed populations or communities. These findings suggest that species' traits play an important role in deterministic species sorting and dispersal processes that will mediate future community responses to global change.

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Chapter 5: Conclusions

Research synthesis and implications

My doctoral research addresses several scientific knowledge gaps concerning the consequences of global change on freshwater ecosystems, with emphasis on the spatial dynamics of stressor resistance in mountain lakes. Major research findings and their implications are discussed below.

Quantitative review

Using a meta-analytic approach, my collaborators and I integrated 286 responses of freshwater ecosystems to paired stressors and discovered that their cumulative mean effect size was less than the sum of their independent effects (i.e. antagonistic) overall (Objective 1a). Antagonism was also the most prevalent interaction type, followed by synergies, simple additive scenarios, and reversals. As anticipated given the diversity of responses, multiple stressor effects varied based on stressor identity and characteristics of the ecological receptor, including response metric, level of biological organization, and organism group (Figs 2.2–2.4; Objective 1b). For instance, the net effects of paired stressors on diversity and functional performance metrics were additive and antagonistic, respectively; suggesting that compensatory dynamics by stress-tolerant organisms may reduce the functional consequences of multiple freshwater stressors. Interestingly, the mean net effects across all stressor pairs and response metrics were consistently antagonistic or additive, in contrast to the greater prevalence of synergies reported in marine systems (e.g. Crain et al. 2008, Harvey et al. 2013, Przeslawski et al. 2015). A possible explanation for greater antagonism between freshwater than marine stressors is that the greater environmental variability of smaller aquatic ecosystems fosters greater adaptive potential.

These meta-analytic findings generate several interesting hypotheses (see *Future Research Directions* below) and have direct conservation applications. Non-additive interactions were far more common than simple additive scenarios; however, knowledge of how specific stressors interact is critical to effectively manage their impacts. For instance, efforts allocated to ameliorating either stressor in a synergistic interaction should yield a significant positive outcome (Brown et al. 2013). Management focusing on either stressor in an additive interaction should also improve conditions, but more effort will be required to achieve a similar level of recovery than for synergies. Antagonistic interactions pose a unique challenge since each stressor may need to be moderated to effectively reduce their combined impact, especially if their independent effects are highly redundant (Brown et al. 2013). Reversals were the least common interaction type; however, these interactions warrant special consideration because they may generate highly unexpected outcomes. For instance, minor stressors may invert the independently positive effects of other co-occurring factors, to deleterious effect. Further, reversal interactions were most commonly associated with warming, suggesting that climate changes may generate more ecological surprises in the future. Generalities uncovered by the meta-analysis can help inform individual management actions focused on alleviating or preventing impacts of multiple ecological stressors and improve global forecasting of freshwater biodiversity and ecosystem functioning scenarios.

Experimental study

Using an experimental approach, I tested the effects of two globally pervasive freshwater stressors, climatic warming and aquatic invasive species, with particular relevance to mountain lake communities. In addition to the independent and combined effects of these stressors, I evaluated the moderating influence of species diversity and the potential for regional species to provide functional rescue effects to species-poor communities. Zooplankton from previously fishless alpine lakes had low resistance against introduced rainbow trout, which significantly reduced taxonomic richness and biomass production; however, warming failed to elicit any significant independent or interacting effects (Fig. 3.1; Objective 2a). In contrast, colonization by several imported stress-tolerant montane species from the regional species pool offset, and eventually reversed, the negative impacts of invasion – resulting in net positive effects on the zooplankton community (Fig. 3.1; Objective 2b). Though access to the regional species pool successfully increased the richness of the prey community, the positive biomass interaction with invasion treatments was driven by the positive responses of a few key taxa. This finding suggests that species identity and functional traits were important in driving biotic resistance (Fig. 3.2; Objective 2c). Further, significant associations between smaller body size and the regional species pool and invasion treatments suggested that community body size distribution is a useful predictor of the impacts of salmonid introductions (Fig. 3.3; Objective 2d). In addition to showing how functional compensation can mediate the consequences of biological invasions, I demonstrated the novel application of a quantitative functional approach as a tool for exploring the direction and magnitude of impacts from multiple ecological stressors.

These experimental findings have clear implications for fisheries management. For instance, my results provide evidence that more diverse communities have greater invasion resistance. This is relevant to environmental agencies, such as Parks Canada, who have long debated the tradeoffs involving exotic sportfish populations and the merits of removing aliens from certain mountain lakes to reestablish their historically fishless state and native species diversity. The reversal interaction, whereby stress-tolerant colonists arriving from the regional species pool overturn the effect of fish, highlights the importance of maintaining habitat connectivity for spatial insurance. These spatial dynamics also show how a metacommunity perspective can alter experimental predictions of stressor impacts, as artificial communities lacking connectivity may respond very differently than those open to dispersal from neighbouring communities. Further, these results reveal the potential utility of assisted species migration for curbing stressor impacts. For instance, stressor-tolerant species may be collected and moved to impacted communities in order to maintain their ecological functioning; however, biological introductions may have unintended consequences and any such actions should be considered carefully.

My experimental results also corroborate certain findings from our quantitative review. Higher temperatures did not interact significantly with the invasion treatment, supporting the meta-analytic finding that invasion × warming interactions are additive overall (Table A-3.1). Further, the meta-analysis indicated a potential for compensatory dynamics to limit the functional impacts of ecological stressors relative to their biodiversity impacts, particularly for animal receptors (Fig. 2.2). The experiment also demonstrated a potential for functional compensation in stressed communities; however, experimental results were driven by spatial insurance rather than stressor co-tolerance.

Observational study

Using an observational approach, historical zooplankton records for 1,234 waterbodies were integrated to evaluate the hierarchical ranking of multiple environmental and spatial factors driving mountain lake zooplankton composition at a continental scale. Zooplankton communities were spatially structured; however, geographic positions explained less species variance than environmental predictors (Fig. 4.3; Objective 3a). The combined effects of catchment/lake morphometry, land cover, and lithology explained more variation in zooplankton beta diversity than climate or fish introduction (Fig. 4.4), but individual climate factors and fish introductions were generally more important than any single climate/lake feature (Fig. 4.5; Objective 3b). The high rankings of climate factors, as well as fish introduction and several climate-sensitive land cover types, indicate potential sensitivity of mountain lake communities to climate change and future biological invasions.

Multispecies connectivity estimates were used to infer dispersal limitation among lake communities and reveal that dispersal processes explained less variation than species sorting along spatially structured environmental gradients (Fig. 4.6; Objective 3c). The importance of dispersal and species sorting processes varied based on species body size and reproductive mode, and larger and obligate sexual copepod species were generally more structured by deterministic community assembly processes (Objective 3d). For instance, larger species were more influenced by temperature and fish introduction, suggesting they may be sensitive to climate warming and biological invasions (Fig. 4.5). Larger and sexual species were also the most structured by patch connectivity, highlighting how they may have limited potential to track changing environmental conditions. In contrast, variation in small and asexual species were less structured by temperature and connectivity, reflecting perhaps their greater dispersal ability and potential for rescue effects on stressed populations or communities (Fig. 4.6; Objective 3e).

Disentangling the multiple sources of variation affecting species composition of communities is a persistent challenge for applied ecologists and biogeographers alike. Efficient use of limited conservation resources necessitates knowledge of both the types of processes affecting ecological communities and their relative importance. Though manipulative experiments provide critical details of stressor impacts in isolation, they often fail to account for spatial dynamics and other confounding factors of natural ecosystems. Thus, by revealing the hierarchical organization of metacommunity drivers across a broad range of lakes, I was able to uncover the tangible effects of local stressors and climatic conditions – providing valuable insights for natural resource and protected areas managers concerned with biodiversity conservation at large spatial scales. Further, my novel assessment of spatial variation among multiple covarying environmental factors advances our theoretical understanding of lake community assembly.

My observational findings also verify several of my experimental results. Foremost, both studies revealed a relatively large independent effect of fish introduction that was mediated by the functional traits of receiving communities. Specifically, findings associated smaller body size with fish tolerance and provided some limited evidence for the importance of predator escape response, which differs between cyclically parthenogenetic asexual and obligate sexual species (Figs 3.3 & 4.5). Similarly, the relationship between body size and temperature detected during the experiment marginally supported that observed in lakes across western North America (Figs 3.3 & 4.5). However, the negligible impact of experimental warming contrasted the high ranking importance of temperature in natural lake communities (Figs 3.1 & 4.5). These conflicting results may have arisen from the low magnitude (1.6°C mean difference) or duration (56 days) of change in warmed mesocosm compared to the 20°C range in 50-year mean annual temperatures estimated for lakes within the study region (Table 4.2). Further, experimental findings suggested that fish introductions can elicit severe local impacts on alpine zooplankton communities, which may be mediated by the arrival of regional fish-tolerant colonists (Fig. 3.1). Though the observational analyses were unable to distinguish among specific mechanisms of spatial dynamics, the lesser importance of fish introductions relative to climate in natural lake communities (Fig. 4.4) may reflect variable invasion resistance along geographic gradients (i.e. greater resistance by montane communities) or rescue effects as natural communities are open to dispersal from neighbouring lakes. Alternatively, predation by native fish species may have pre-conditioned communities in certain stocked lakes to the impacts of exotic planktivores. Both the observational and experimental studies point to the importance of spatial dynamics for stressor resistance, as dispersal permits species to colonize novel habitats and track environmental changes. My research also highlights the importance of metacommunity functional structure, as species traits controlling stressor tolerance and dispersal ability will dictate the winners and losers of global change scenarios and their functional consequences.

Future research directions

My thesis findings evoke several testable hypotheses and future research considerations, including:

1) Whether higher temperature, UVR exposure, and nutrification synergistically stimulate primary production. The meta-analytic results indicate a possible synergy; however, future studies should investigate the potential for these stressors to increase the prevalence or magnitude of deleterious algal blooms.

2) Whether functional endpoints are consistently less sensitive than species diversity to the effects of multiple ecological stressors. The meta-analytic results indicate differing sensitivities between response metrics; however, future studies should investgate the extent of functional compensation in freshwaters and whether compensatory dynamics are more prevalent under specific circumstances.

3) Which specific mechanisms drive antagonism among freshwater stressors. The meta-analytic results indicate that antagonism is prevalent in freshwaters; however, future studies should investigate whether this result is most commonly linked to asymmetry of stressor magnitudes, hard selection for co-adapted organisms, or similarity in behavioural or physiological acclimation, and whether mechanisms vary depending on characteristics of the stressors or biological response.

4) Why freshwaters are less sensitive to multiple stressor effects than marine ecosystems. Comparison of the meta-analytic results with previous reports suggests a disparity between freshwater and marine ecosystems; however, future studies should consider the potential physiological, genetic, spatial, or environmental drivers for perceived differences.

5) How the nature of multiple stressor interactions vary within more detailed stressor and receptor classes. The meta-analytic results show trends in stressor interactions across broad categories (e.g. habitat alteration and biological invasion); however, as additional experimental responses become available, future studies should examine further sources of heterogeneity. For instance, experiments may consider whether interactions involving biological invasions differ if the invader is a predator or a competitor, or whether interactions with habitat alteration vary baesd on the type of alteration.

6) Whether stressor interactions involving greater numbers of stressors lead to deleterious synergistic meltdowns. The prevalence of antagonism involving freshwater stressor pairs indicates a certain resistance or co-tolerance to multiple stressors; however, as additional experimental responses become available, future studies should examine whether increasing numbers of stressors weaken biological resistance and generate more detrimental feedbacks.

7) Whether the nature of multiple stressor interactions vary based on stressor magnitudes. Both the meta-analytic and experimental results fail to address how variations in stressor magnitude, for instance degree of temperature increase or rate of predation by biological invaders, influence the outcome of multiple stressor interactions; however, future studies should consider this potential moderator.

   a) Future studies should investigate whether predictable thresholds exist where increasing stressor magnitudes overwhelm the resistance of biological receptors and switch the outcome of their interactions.

   b) Future studies should scrutinize potential thresholds involving temperature variations, given the global relevance of climate warming and the potential for higher temperatures to generate problematic reversal interactions. Manipulative experiments should focus on realistic stressor magnitudes for future global change scenarios.

8) Whether the nature of multiple stressor interactions vary based on the order of stressor application. Both the meta-analytic and experimental results fail to address how the sequential application of stressors might pre-condition biological receptors for subsequent pressures and influence the outcome of multiple stressor interactions; however, future studies should consider this potential moderator.

9) Whether the nature of stressor interactions vary based on duration of stressor exposure. Both the meta-analytic and experimental results fail to address how exposure time might influence the outcome of multiple stressor interactions; however, future studies should consider this potential moderator.

   a) Future studies should utilize species with rapid reproductive rates and consider stressor impacts over several generations to assess potential evolutionary responses.

10) Whether the nature of stressor interactions vary based on community connectivity. The meta-analytic results fail to address how dispersal processes might influence the outcome of multiple stressor interactions; however, based on experimental findings indicating the importance of spatial insurance, future studies should consider this potential moderator.

11) Whether species plasticity mediates functional stressor resistance. The experimental results fail to adress the potential role of intraspecific trait variation in mediating stressor response; however, future studies should consider the importance of species plasticity for increasing response diversity.

12) Whether habitat complexity mediates functional stressor resistance. The experimental results fail to address the role of physical habitat structure in mediating stressor response; however, future studies should consider the importance of habitat (e.g. depth and macrophyte refugia) for providing organisms opportunities to avoid stressors.

13) Which specific mechanisms relate terrestrial–aquatic linkages and climate filters to species composition. The observational results suggest that topography, land cover, lithology, and climate factors (especially precipitation) play important roles in driving beta diversity at large spatial scales; however, future studies should evaluate the specific mechanisms (e.g. hydrological controls or water quality effects) responsible for observed patterns.

14) How species composition patterns are affected by interactions among ecological stressors and community assembly processes at large spatial scales. The meta-analytic results indicate that multiple stressor impacts are frequently non-additive; however, the observational results fail to address potential interactions among multiple covarying metacommunity predictors. Future studies should quantify interactions between relevant environmental and spatial parameters, including cross-scale interactions between local and regional factors.

15) Which factors mediate the predatory effects of exotic sportfish across lakes. The observational results suggest that fish introductions explain less species variance than indicated by the experimental results; however, neither study reflects heterogeneity in fish communities. Future studies should consider how fish impacts differ based on species identity, variation in stocking density, time since initial stocking event, and the potential influence of native fish populations where present (e.g. greater food web complexity with native piscovores).

16) How the composition of mountain lake communities have been altered by recent climate changes. The observational results were robust to variation in sampling date; however, better temporal data would permit future studies to consider how lake communities and environmental variables have changed over time.

17) How species dispersal is limited by the topographic complexities of mountain regions. The observational study evaluated connectivity based on planar distances between occupied lake habitats; however, future studies should consider topographic dispersal barriers (i.e. mountain ridges) and how they modify spatial dynamics.

    a) Future studies should investigate zooplankton affinity for specific dispersal vectors (e.g. individual species or groups of waterbirds) and evaluate whether topographic barriers limit their movement. For instance, there are knowledge gaps concerning the selection of waterbodies by migratory birds along elevation gradients and whether climate change will influence their usage of alpine habitats in the future.

b) Future studies should improve connectivity estimates by supplementing analysis of species distributions with molecular analysis of population genetic dissimilarities.

c) Future studies should address the uncertainty regarding potential dispersal limitation and rescue effects in alpine communities by evaluating the merit, feasibility, and potentially unintended consequences of assisted species migration to maintain ecosystem functioning at high elevations and latitudes.

d) Future studies should use natural ecosystems along elevation gradients for long-term manipulative experiments to enhance our knowledge of community assembly and the potential for rescue effects to curb the functional consequences of global change.

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Appendix A: Supplemental information for chapter 2

Appendix A-1: Meta-analytic data references

Full list of data references used in meta-analyses:

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Appendix A-2: Sensitivity analyses

Publication bias

A common concern with contemporary meta-analyses is the potential for publication bias to influence mean effect size calculations (Nakagawa & Santos 2012). Publication bias is typically propagated by the greater likelihood of publication for experiments with significant results, which may skew meta-analytic findings (Rosenthal 1979). To test for publication bias and assess its potential impact on our results, we used the following multistep approach.

First, we evaluated our data graphically with funnel plots comparing our standardized interaction effect sizes against their pooled sample sizes (calculated as $n_p + n_o$, where n_p was calculated as $n_A + n_B$ and $n_o = n_{AB}$) and estimated precision (1/variance; Fig. A-2.1). Here, significant asymmetry around the mean interaction effect size may indicate publication bias; however, asymmetry may also be caused by chance or by true heterogeneity in the dataset (Nakagawa & Santos 2012).

Visual assessment of our funnel plots suggested a potential bias towards negative (antagonistic) interaction effect sizes, as indicated by outlying data points (Fig. A-2.1a, b). We followed this visual assessment with Spearman rank correlation and Eggers regression tests to statistically evaluate data asymmetry, using MetaWin Version 2.1 (Rosenberg et al. 2000) and the ‘metafor’ package (Viechtbauer 2010) in the R computing program (R Core Team 2016), respectively. Statistically significant correlations/regressions may indicate publication bias towards larger effect sizes (Begg 1994, Egger 1997). Results of Spearman rank correlation tests indicated a significant relationship between effect size and variance ($n = 286$, $r_s = –0.254$, $P < 0.001$) and a non-significant relationship between effect size and pooled sample size ($n = 286$, $r_s = 0.016$, $P = 0.794$). Similarly, the Eggers regression tests indicated a significant relationship between effect size and standard error ($n = 286$, $z = –10.370$, $P = <0.001$) and a non-significant relationship between effect size and pooled sample size ($n = 286$, $z = –1.153$, $P = 0.249$).

Although our funnel plot assessments and regression/correlation-based tests both indicated significant asymmetry in our dataset, these results do not necessarily indicate significant publication bias as data asymmetry may also be attributable to chance or true heterogeneity in the dataset (Nakagawa & Santos 2012). Thus, these results require careful interpretation with consideration of the total amount of heterogeneity present and whether publication bias is in fact the most reasonable mechanism to explain the specific asymmetries observed. For instance, our results suggest a potential bias towards negative interaction effects sizes (and antagonisms); however, we might intuitively expect that interactions involving synergies would have a greater likelihood of being over-reported in the literature because they represent more dramatic scenarios. Further, we compare a diverse set of measurements from stressor experiments on different organism groups and across levels of biological organization in our global meta-analysis, and thus the considerable heterogeneity observed in this analysis (Q_{total} = 912.70) was expected. To explain this variance we used a series of mixed effects categorical meta-analyses using biologically relevant moderators. Indeed, we found that levels of these moderators varied in their mean effect sizes (see Table A-3.1 in Appendix A-3), reflecting the variable responses of the groups to multiple stressor impacts.

Nevertheless, we conducted a series of tests to assess the sensitivity of our global meta-analysis to effect size outliers (potential publication bias). First, we used Rosenthal's method to estimate a fail-safe number, which is the number of nonsignificant or missing observations that would be needed to change the significance of our findings (Rosenthal 1979). A fail-safe number larger than $5(n) + 10$ (where n is the number of studies in the meta-analysis) is generally considered to be robust against publication bias (Rosenthal 1979). We used MetaWin Version 2.1 (Rosenberg et al. 2000) to estimate a fail-safe number of 24,797, which far exceeds the minimum recommended number based on our sample size (24,797 > 1,440). This suggests that our overall estimate is reliable, even with the observed data asymmetry. Secondly, we used the 'metafor' package (Viechtbauer 2010) in the R computing program (R Core Team 2016) to conduct a trim and fill analysis. Similar to the fail-safe number, this approach is used to assess the impact of potentially missing observations on the meta-analytic results (Nakagawa & Santos 2012). However, trim and fill analysis failed to identify any missing studies needed to restore symmetry (missing studies = 0), though it performed poorly ($P = 0.50$ that the model estimated the correct number of missing studies), likely owing to the considerable heterogeneity in our dataset.

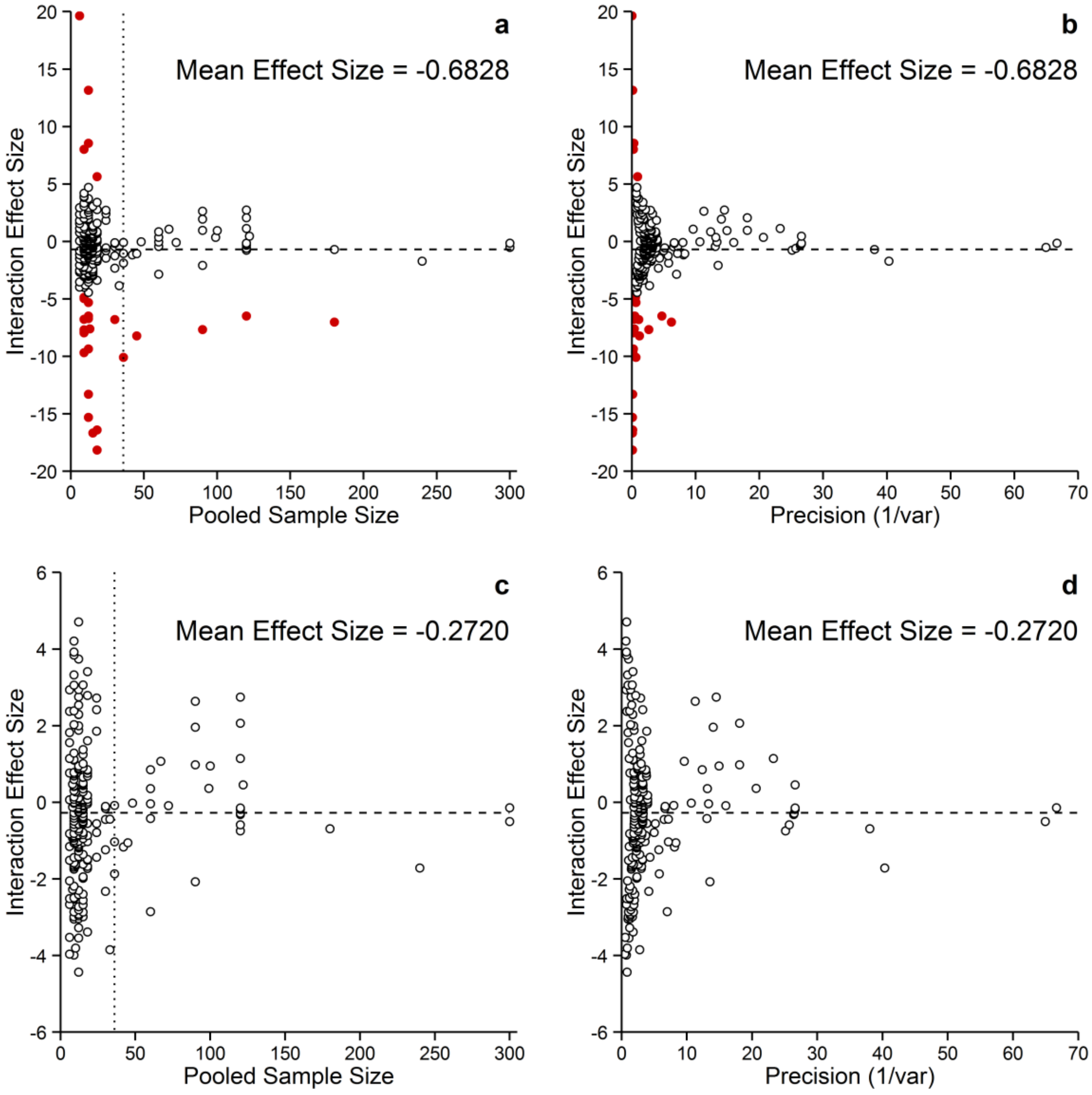

Fig. A-2.1 Funnel plots of standardized interaction effect sizes (Hedge's *d*) against pooled sample sizes (a and c) and precision estimates (b and d). Plots (a) and (b) present our entire dataset (*n* = 286; 13 data points not shown where effect sizes >20 (*n* = 4) or <20 (*n* = 9)) and plots (c) and (d) present our dataset reduced to test for sensitivity to outlying effect sizes and potential publication bias (*n* = 245). Effect sizes omitted for our publication bias sensitivity analysis are coloured red (a and b); dashed horizontal lines indicate weighted mean interaction effect sizes; and dotted vertical lines indicate a pooled sample size of 26 (used as a cut-off to reduce our dataset for our sample size sensitivity analysis).

Finally, to demonstrate the robustness of our global meta-analytic findings in spite of any publication bias, we re-analyzed our dataset after omitting potential effect size outliers. We identified 41 potential effect size outliers based on a visual assessment of our funnel plots (red data points in Fig. A-2.1a, b). Even after removing these data points, our random effects model found a significantly antagonistic mean net effect (*d* = –0.2720 with upper and lower bootstrapped confidence intervals of –0.4602 and –0.0877, respectively; Fig. A-2.1c, d). Together, these results suggest that our meta-analytic findings are robust to data asymmetry, regardless of whether the observed pattern reflects publication bias or true heterogeneity.

Table A-2.1 Mean interaction effect sizes for levels of moderators where more than three studies were omitted after excluding those studies with large sample sizes (replication ≥ 12 or pooled sample ≥ 26). *n* = group sample size; *d* = mean effect size; CI = 95% bootstrapped confidence intervals; and Interaction = mean interaction type.

	Full dataset			Reduced dataset			
Analysis / level	*n*	*d*	CI	*n*	*d*	CI	Interaction
Global analysis	230	-0.65	-0.95 to -0.33	202	-0.69	-1.04 to -0.36	Antagonistic
Level of organization							
Population	70	-0.60	-1.21 to 0.08	55	-0.66	-1.04 to 0.16	Additive
Organism	23	-0.91	-1.47 to -0.41	10	-1.43	-2.63 to -0.53	Antagonistic
Stressor-Pair							
Contamination x Habitat alteration	19	-0.25	-1.07 to 0.86	16	-0.09	-1.04 to 1.26	Additive
Contamination x Warming	33	-0.87	-1.69 to -0.18	18	-1.34	-2.43 to -0.39	Antagonistic
Response Level							
Vertebrate	56	-0.62	-1.15 to -0.10	37	-0.75	-1.32 to -0.16	Antagonistic

Sample size

Similar to the publication bias sensitivity analysis, we explored the sensitivity of our analyses to variation in study sample size. Specifically, observations with larger sample sizes are expected to have lower variance and thus carry more weight in our meta-analytic models. To test the robustness of our dataset to such variations, we explored how observations with large sample sizes (control replication of ≥ 12 or pooled sample size ≥ 26) may skew our results by reanalyzing our data with these points omitted (*n* = 28; Fig. A-2.1a, c). We found that the mean effect size did not change significantly overall, or in any categorical grouping (where at least three studies were omitted; Table A-2.1). Since the mean effect sizes were similar to those calculated based on our entire dataset, and none of the interaction type assignments changed (Table A-2.1), this further demonstrates the robustness of our meta-analytic results.

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Appendix A-3: Detailed meta-analytic results

Table A-3.1 Summary statistics for meta-analytic models.

Model	Dataset	Fixed effect	Level of fixed effects	*n*	*d*	L CI	U CI	INT	$\hat{\sigma}^2_{pooled}$
1) Full global	Full	---	**Overall**	**286**	**-0.68**	**-0.94**	**-0.41**	**Ant**	**2.58**
2) Detailed response metric	Full	Detailed response metric	Animal biomass / abundance	68	-0.85	-1.34	-0.37	Ant	1.99
			Animal condition	17	-1.01	-1.65	-0.51	Ant	0.40
			Animal diversity	22	-0.27	-0.95	0.35	Add	1.44
			Animal growth / size	30	-0.94	-1.98	-0.16	Ant	2.99
			Animal survival	30	-1.34	-2.69	-0.18	Ant	6.30
			Behaviour	4	-1.16	-2.90	0.41	Add	3.03
			Decomposition	14	0.12	-0.83	1.36	Add	2.88
			Other biomass / abundance	4	0.45	-0.73	1.84	Add	1.21
			Other survival	2	-1.95	-4.86	0.14	Add	11.35
			Plant biomass / abundance	66	-0.58	-1.21	0.02	Add	3.80
			Plant diversity	9	-0.87	-1.35	-0.44	Ant	0.00
			Plant growth / size	16	0.57	-0.99	2.40	Add	6.92
			Reproductivity	4	-0.86	-1.51	-0.30	Ant	0.27
			Overall	**286**	**-0.69**	**-0.96**	**-0.42**	**Ant**	**2.86**
3) Pooled response metric	Full	Pooled response metric	Diversity	31	-0.44	-0.96	0.06	Add	1.11
			Functional performance	255	-0.72	-1.03	-0.42	Ant	2.68
			Overall	**286**	**-0.68**	**-0.97**	**-0.42**	**Ant**	**2.59**
4) Reduced global	Reduced	---	**Overall**	**230**	**-0.65**	**-0.96**	**-0.34**	**Ant**	**2.76**
5) Response level	Reduced	Level biological organization	Community	137	-0.63	-0.98	-0.27	Ant	3.01
			Organism	23	-0.91	-1.47	-0.41	Ant	0.50
			Population	70	-0.60	-1.21	0.08	Add	4.72
			Overall	**230**	**-0.65**	**-0.95**	**-0.34**	**Ant**	**2.84**
6) Oransim group	Reduced	Organism group	Bacteria	2	0.32	0.14	0.49	Syn	-0.34
			Fungi	2	0.72	-1.06	2.54	Add	5.89
			Invertebrate	73	-1.18	-1.75	-0.66	Ant	2.76
			Producer	95	-0.30	-0.80	0.22	Add	4.07
			Vertebrate	56	-0.62	-1.15	-0.10	Ant	2.42
			Virus	2	-1.18	-2.66	-0.07	Ant	2.54
			Overall	**230**	**-0.65**	**-0.96**	**-0.33**	**Ant**	**2.82**
7) Stressor pairs	Reduced	Stressor-pair	Acidification x Contamination	3	-1.08	-1.86	0.28	Add	1.03

Model	Dataset	Fixed effect	Level of fixed effects	n	d	L CI	U CI	INT	$\hat{\sigma}^2_{pooled}$
			Acidification x Habitat Alteration	2	-4.80	-7.95	-2.98	Ant	9.81
			Acidification x UVR	3	2.45	-0.50	19.65	Add	17.20
			Acidification x Warming	5	-0.81	-3.54	0.44	Add	1.20
			Contamination x Contamination	6	-2.17	-4.39	-0.36	Ant	2.10
			Contamination x Habitat Alteration	19	-0.25	-1.07	0.86	Add	3.87
			Contamination x Invasion	11	-1.40	-2.92	-0.20	Ant	9.16
			Contamination x Nutrification	14	-0.19	-1.94	1.31	Add	4.59
			Contamination x UVR	6	-0.46	-1.41	0.22	Add	0.57
			Contamination x Warming	33	-0.87	-1.69	-0.19	Ant	1.54
			Habitat Alteration x Habitat Alteration	4	-1.02	-3.84	2.02	Add	8.08
			Habitat Alteration x Invasion	2	-2.51	-2.73	-2.30	Ant	-0.55
			Habitat Alteration x Nutrification	21	-0.13	-1.15	0.82	Add	3.02
			Habitat Alteration x Warming	6	-2.35	-4.60	-0.94	Ant	2.65
			Invasion x Invasion	13	-0.43	-0.95	0.02	Add	0.91
			Invasion x Nutrification	10	-0.70	-4.06	1.38	Add	12.84
			Invasion x Warming	7	-0.40	-0.88	0.18	Add	0.22
			Nutrification x UVR	10	0.23	-2.12	2.24	Add	9.13
			Nutrification x Warming	41	-0.46	-1.38	0.39	Add	5.10
			Warming x UVR	13	-0.99	-1.79	-0.21	Ant	0.81
			Overall	**229**	**-0.67**	**-0.97**	**-0.37**	**Ant**	**3.16**

Note: models 1 and 4 are global random effects meta-analytic models using observation ID as a random effect; Models 2–3 and 5–7 are mixed effects meta-analytic models using observation ID as a random effect and the categorical moderators as fixed effects; reduced dataset is most inclusive response metric dataset; *n* = number of the studies; *d* = mean interaction effect size; L CI and U CL = lower and upper bootstrapped 95% confidence interval; INT = assigned interaction type, where Ant = antagonistic, Add = additive, and Syn = synergistic; $\hat{\sigma}^2_{pooled}$ = pooled variance; and dashes denote no fixed effect in meta-analytic model.

Table A-3.2 Heterogeneity estimates for meta-analytic models.

Model	Total heterogeneity	Between-class heterogeneity	Within-class heterogeneity
1) Full global	912.70	--	--
2) Detailed response metric	874.40	18.49	855.91
3) Pooled response metric	911.47	0.67	910.80
4) Reduced global	736.77	--	--
5) Response level	729.23	0.57	728.66
6) Organism group	731.14	10.44	720.70
7) Stressor pairs	699.24	29.10	670.15

Note: dashes denote value not applicable.

Appendix B: Supplemental information for chapter 3

Appendix B-1: Sampling locations

Table B-1.1 Waterbodies sampled for local and regional species pools.

Lake ID	Species pool	Ecoregion	Location	Fish present	Easting (m)	Northing (m)	Elevation (masl)	Temp (°C)	Max depth (m)
Bighorn Lake	Local	Alpine	Banff	No	593902	5702351	2353	9.7[a]	9.2[a]
Pipit Lake	Local	Alpine	Banff	No	578772	5719046	2226	10.8[a]	20.6[a]
Snowflake Lake	Local	Alpine	Banff	No	580862	5716976	2347	12.2[a]	12.5[a]
3 Lakes Valley Lower Lake	Regional A	Subalpine	Peter Lougheed	No	621449	5631198	2299	16.1	<2.0
3 Lakes Valley Pond	Regional A	Subalpine	Peter Lougheed	No	621064	5630928	2262	11.9	2.5
Burstall Lake	Regional A	Montane	Peter Lougheed	Yes	617324	5626895	1953	12.3	6.0
Chester Lake	Regional A	Subalpine	Peter Lougheed	Yes	621614	5630327	2244	14.0	13.2
Copper Lake	Regional A	Montane	Banff	Yes	575145	5679342	1430	19.9	11.0
East Ridge Pond #1	Regional A	Alpine	Banff	No	582006	5717765	2300[a]	NM	<2.0
Gully Pond #1	Regional A	Alpine	Banff	No	581807	5717727	2249	NM	<2.0
Herbert Lake	Regional A	Montane	Banff	Yes	553950	5701253	1652	15.7[a]	13.3[a]
Johnson Lake	Regional A	Montane	Banff	Yes	605893	5672786	1419	19.5	2.6
Kingfisher Pond	Regional A	Montane	Banff	Yes	558000	5696395	1591	18.0[a]	6.1[a]
Little Herbert Lake	Regional A	Montane	Banff	Yes	554430	5700345	1585	17.1[a]	8.2[a]
Plateau Pond A	Regional A	Alpine	Banff	No	571611	5692591	2687	15.4	<2.0
Smith Lake	Regional A	Montane	Banff	Yes	574985	5678141	1560	18.2	9.0
Snowflake Pond	Regional A	Alpine	Banff	No	581417	5717972	2289	15.5	<2.0
Two Jack Lake	Regional A	Montane	Banff	Yes	604917	5676089	1495	20.2	12.1
Daer Lake	Regional B	Montane	Kootenay	No	574024	5627729	1165	18.9	<2.0
Dog Lake	Regional B	Montane	Kootenay	Yes	575486	5626002	1200	20.6	3.8
Emerald Lake	Regional B	Montane	Yoho	Yes	532511	5699190	1303	15.7	20.0

Lake ID	**Species pool**	**Ecoregion**	**Location**	**Fish present**	**Easting (m)**	**Northing (m)**	**Elevation (masl)**	**Temp (°C)**	**Max depth (m)**
K4 Pond	Regional B	Montane	Kootenay	No	575805	5625299	1194	21.5	<2.0
Kootenay Pond	Regional B	Montane	Kootenay	Yes	567391	5638269	1182	20.4	8.8
Moraine Lake	Regional B	Subalpine	Banff	Yes	556926	5686097	1870	10.4	7.0
Sherbrooke Lake	Regional B	Subalpine	Yoho	Yes	542590	5700624	1801	11.5	6.3
Upper Waterfowl Lake	Regional B	Montane	Banff	Yes	525336	5744252	1662	11.2	8.3
Vista Lake	Regional B	Montane	Banff	Yes	568252	5676861	1571	16.1	6.3
Wapta Lake	Regional B	Montane	Yoho	Yes	545010	5698867	1588	10.8	7.3

Note: northing and easting coordinates are Zone 11 Universal Transverse Mercator (UTM), North American Datum (NAD) of 1983; elevations are reported as metres above sea level (masl); temp refers to near-surface temperature measurements collected at the time of sampling; NM indicates temperature measurements were not collected; and ^{a} denotes measurement obtained from historical summer survey.

Appendix B-2: Surface water temperatures

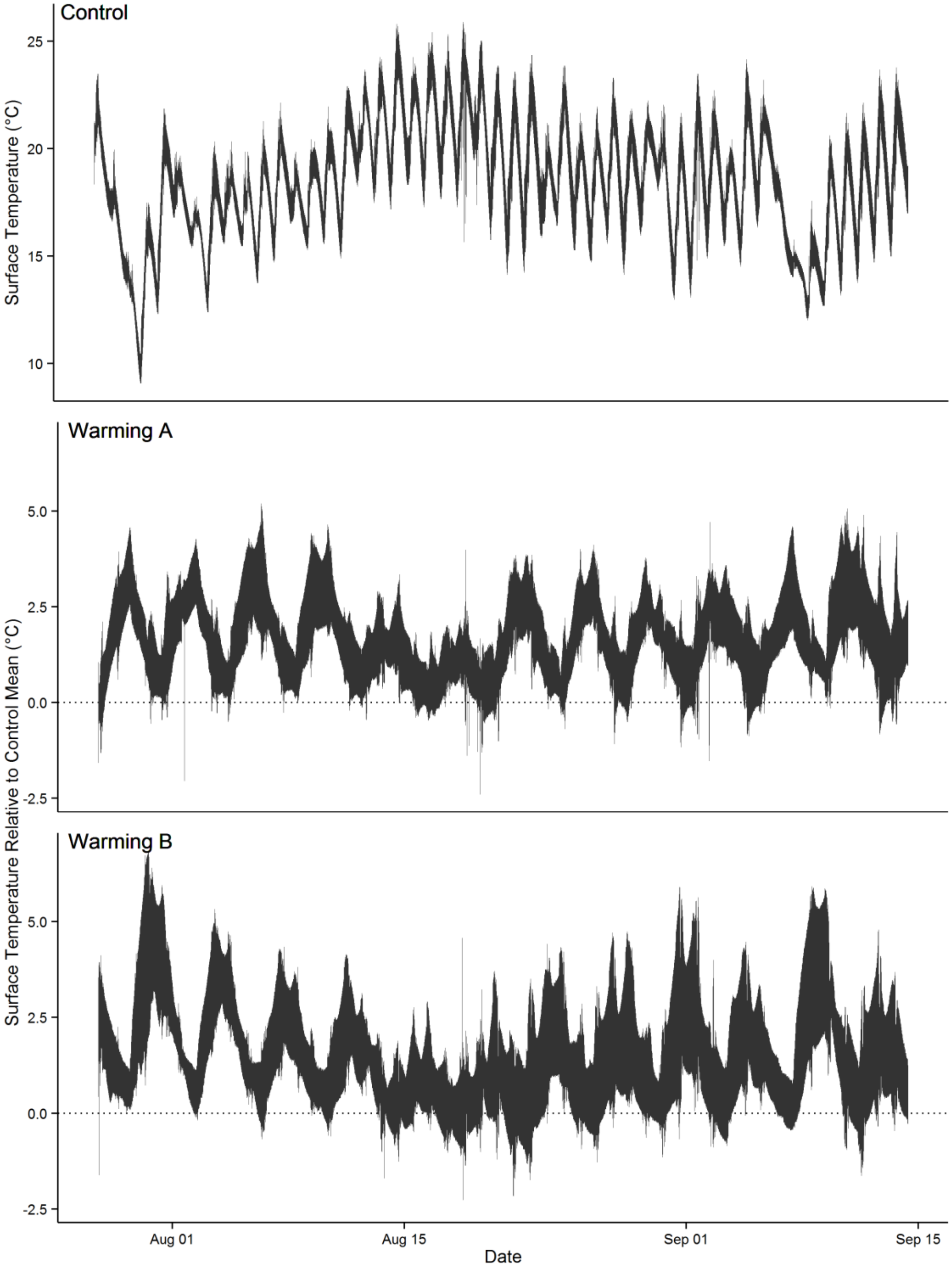

Fig. B-2.1 Surface temperatures in mesocosms over time. Data ranges for each group of replicates are reported relative to mean control temperatures for warmed tanks. Warming A and B denote mesocosm groups that alternatively received 48-h periods of heating.

Appendix B-3: *Chaoborus* larvae biomass

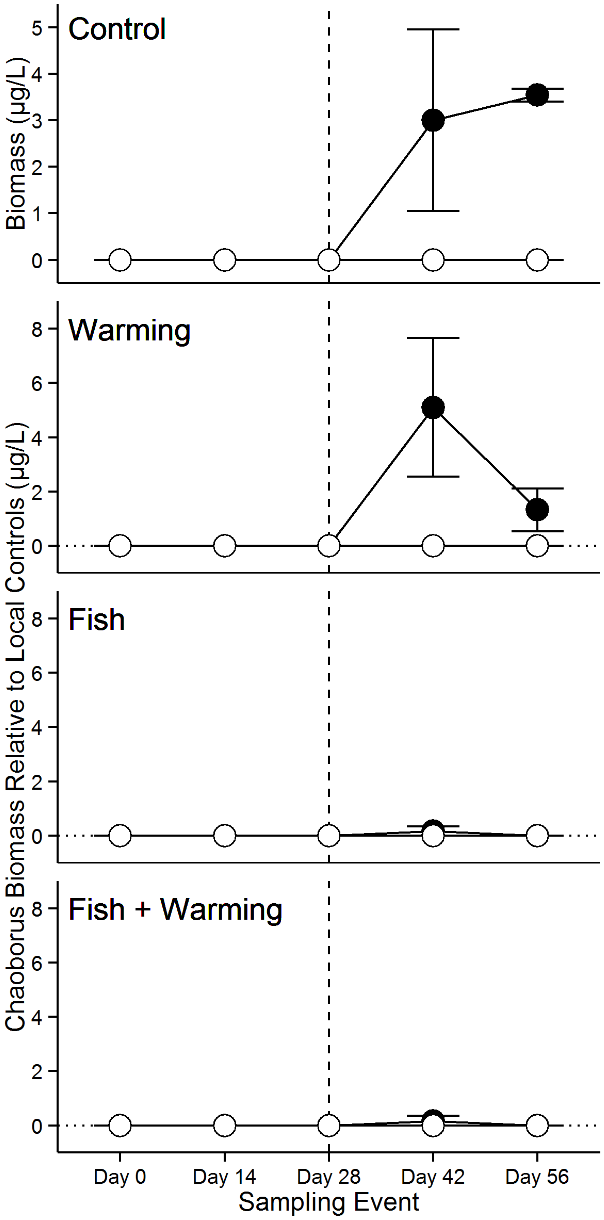

Fig. B-3.1 *Chaoborus* larvae biomass in mesocosms over time. Stressor effects on *Chaoborus* in local (white circles) and regional (black circles) communities were compared against stressor free controls with local zooplankton species only. Vertical line represents application of regional dispersers. Data are mean values ± 1 standard error (SE) of the difference between sample means (*n* = 8 for days 0–28, except *n* = 7 for Fish + Warming on day 28; and *n* = 4 for days 42–56, except *n* = 3 for Fish + Warming + Local Species Only).

Appendix B-4: Algal community assessment

Sample collection and analysis

Phytoplankton (free-floating algae) samples were collected from the water column of each mesocosm concurrent to the collection of zooplankton samples (i.e. days 0, 14, 28, 42 and 56). To concentrate phytoplankton, 500–1000 mL of water was filtered on to Whatman GF/F filter papers for each sample. Periphyton (attached algae) was sampled from each mesocosm at the middle (day 28) and end (day 56) of the experiment. Samples were obtained by pressing 3.8 cm diameter felt pads against the mesocosm floors using a wooden stick and slowly rotating to scrape off and collect algae beneath the pad. For each sampling event, three replicate periphyton samples were obtained from each mesocosm. Phytoplankton filters and periphyton pads 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 concentrations were measured as a proxy for algae abundance/biomass using high-performance liquid chromatography (HPLC) following standard methods (described by Vinebrooke & Leavitt 1999).

The effects of treatments on total chlorophyll concentrations in phytoplankton and periphyton communities were analyzed for each sampling date using parametric analysis of variance (ANOVA). Data were $\log_{10}(x+1)$ transformed prior to analysis and the value of α was adjusted from 0.05 to 0.01 using a Bonferroni correction to account for multiple comparisons.

Results

Total chlorophyll concentrations in phytoplankton communities were similar among mesocosms (mean = 0.18 μg/L) on day 0, prior to the application of experimental treatments (Fig. B-4.1). Warming did not significantly affect phytoplankton communities; however, the presence of fish significantly increased total chlorophyll concentrations on each sampling event (Fig. B-4.1; Table B-4.1). There was a significant interaction between warming and fish on phytoplankton on day 28, where the effect of fish only occurred under warmed conditions (Fig. B-4.1; Table B-4.1). The addition of regional zooplankton species after day 28 had no significant effect on phytoplankton communities (Fig. B-4.1; Table B-4.1). Similarly, fish presence significantly increased total chlorophyll concentrations in periphyton communities, while warming and regional zooplankton species had no significant effects (Fig. B-4.2; Table B-4.2).

Table B-4.1 Results of ANOVA for total phytoplankton chlorophyll concentrations over time.

Event	Treatment	SS	df	*F*	*P* (>*F*)
Day 0	Fish presence	0.0011	1	0.160	0.692
	Temperature	0.0001	1	0.016	0.900
	F x T	0.0401	1	5.855	0.022
	Error	0.1918	28	---	---
Day 14	Fish presence	1.8211	1	14.813	**0.001***
	Temperature	0.0153	1	0.124	0.727
	F x T	0.0017	1	0.014	0.906
	Error	3.4424	28	---	---
Day 28	Fish presence	0.6312	1	10.238	**0.004***
	Temperature	0.3346	1	5.427	0.028
	F x T	0.7659	1	12.422	**0.002***
	Error	1.6647	27	---	---
Day 42	Fish presence	0.8157	1	18.879	**<0.001***
	Temperature	0.0503	1	1.165	0.292
	Species pool	0.0750	1	1.737	0.201
	F x T	0.0652	1	1.509	0.232
	F x P	0.0149	1	0.345	0.563
	T x P	0.0714	1	1.652	0.212
	F x T x P	0.0649	1	1.502	0.233
	Error	0.9938	23	---	---
Day 56	Fish presence	0.6422	1	21.010	**<0.001***
	Temperature	0.0265	1	0.868	0.361
	Species pool	0.0128	1	0.420	0.523
	F x T	0.0299	1	0.979	0.333
	F x P	0.0158	1	0.518	0.479
	T x P	0.0203	1	0.663	0.424
	F x T x P	0.0338	1	1.106	0.304
	Error	0.7030	23	---	---

Note: boldface type and * denote significance at $\alpha = 0.01$ (Bonferroni-adjusted); F = Fish Presence; T = Temperature; P = Species Pool; and dashes denote values are not applicable.

Table B-4.2 Results of ANOVA for total periphyton chlorophyll concentrations over time.

Event	Treatment	*SS*	*df*	*F*	*P* (>*F*)
Day 28	Fish presence	2.4779	1	56.148	**<0.001***
	Temperature	0.0189	1	0.427	0.519
	F x T	<0.0001	1	0.001	0.980
	Error	1.1474	26	---	---
Day 56	Fish presence	0.5275	1	7.798	**0.010***
	Temperature	0.0353	1	0.521	0.478
	Species pool	0.0416	1	0.615	0.441
	F x T	0.0029	1	0.042	0.839
	F x P	0.0007	1	0.010	0.922
	T x P	0.0527	1	0.779	0.387
	F x T x P	0.0645	1	0.953	0.339
	Error	1.5559	23	---	---

Note: boldface type and * denote significance at $\alpha = 0.01$ (Bonferroni-adjusted); F = Fish Presence; T = Temperature; P = Species Pool; and dashes denote values are not applicable.

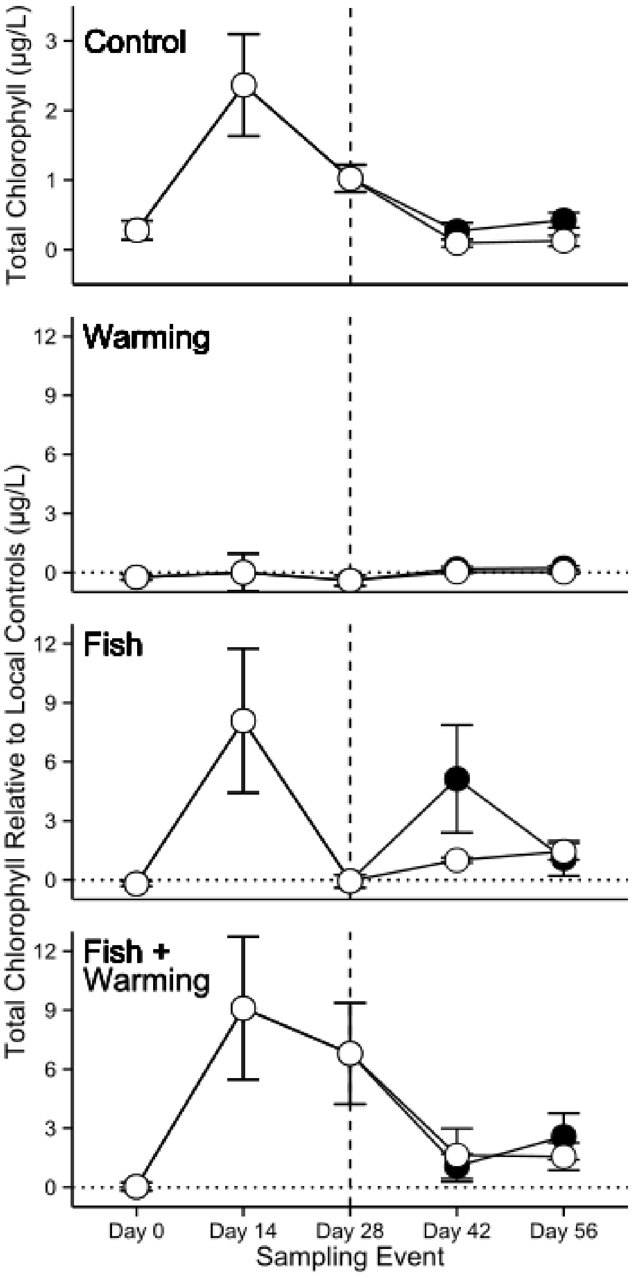

Fig. B-4.1 Total chlorophyll concentrations in phytoplankton communities over time. Stressor effects on mesocosms with local (white circles) and regional (black circle) zooplankton species pools were compared against stressor free controls with local zooplankton species only. Vertical line represents application of regional dispersers. Data are mean values ± 1 standard error (SE) of the difference between sample means (*n* = 8 for days 0–28, except *n* = 7 for Fish + Warming on day 28; and *n* = 4 for days 42–56, except *n* = 3 for Fish + Warming + Local Species Only).

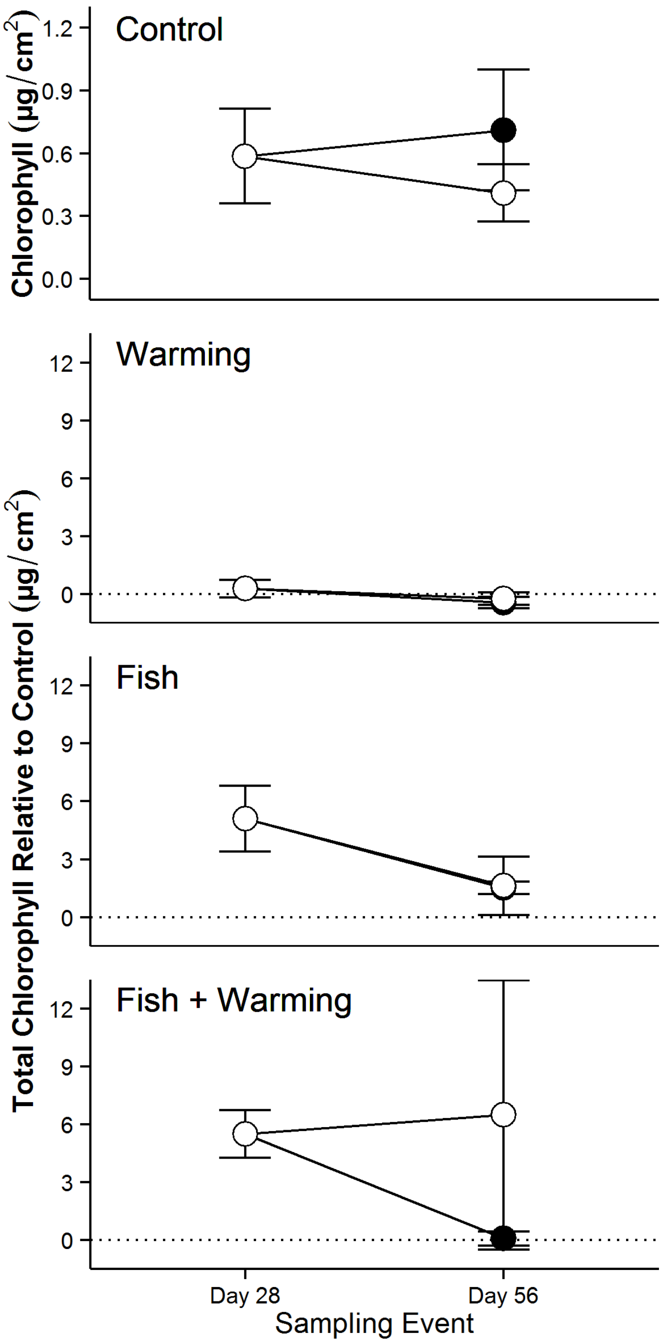

Fig. B-4.2 Total chlorophyll concentrations in periphyton communities over time. Stressor effects on mesocosms with local (white circles) and regional (black circle) zooplankton species pools were compared against stressor free controls with local zooplankton species only. Data are mean values ± 1 standard error (SE) of the difference between sample means (*n* = 8 for day 28, except *n* = 7 for Fish and Fish + Warming; and *n* = 4 for day 56, except *n* = 3 for Fish + Warming + Local Species Only).

Literature cited

Vinebrooke RD & Leavitt PR. (1999) Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based approach. *Journal of the North American Benthological Society*, 18, 15–33.

Appendix B-5: Detailed statistical results

Table B-5.1 MANOVA table (part 1) summarizing the significance of treatment main effects on final taxa biomass.

	Fish presence		Temperature		Species pool	
Analysis	*F*	*P* (>*F*)	*F*	*P* (>*F*)	*F*	*P* (>*F*)
Full multivariate analysis	126.22	**0.001***	7.40	0.916	168.96	**0.001***
Arctodiaptomus arapahoensis	3.51	0.292	0.06	0.967	2.26	0.403
Acanthocyclops vernalis complex	11.77	**0.019***	0.51	0.799	8.75	**0.042***
Acanthodiaptomus denticornis	2.72	0.343	0.31	0.869	12.30	**0.013***
Aglaodiaptomus leptopus	0.06	0.967	0.57	0.828	5.86	0.051
Bosmina longirostris	11.00	**0.013***	0.03	0.971	11.24	**0.008***
Ceriodaphnia quadrangula	12.91	**0.008***	0.60	0.799	15.00	**0.008***
Chydorus sphaericus	11.94	**0.008***	0.12	0.939	12.45	**0.008***
Daphnia spp.	57.08	**0.008***	0.42	0.828	3.28	0.280
D. middendorffiana	--	--	--	--	--	--
D. pulex	--	--	--	--	--	--
D. mendotae	--	--	--	--	--	--
D. dentifera	--	--	--	--	--	--
D. unidentified	--	--	--	--	--	--
Diacyclops navus	--	--	--	--	--	--
Diacyclops thomasi	9.80	**0.013***	0.44	0.846	19.52	**0.008***
Diaphanosoma birgei	1.61	0.280	0.41	0.967	1.14	0.665
Eucyclops agilis	10.37	**0.008***	0.10	0.941	2.26	0.392
Hesperodiaptomus arcticus	6.07	0.090	0.01	0.971	8.68	**0.040***
Leptodiaptomus nudus	1.74	0.516	1.41	0.498	5.74	**0.048***
Leptodiaptomus sicilis	1.06	0.806	0.09	0.925	3.21	0.280
Leptodiaptomus tyrrelli	1.80	0.464	2.05	0.434	22.08	**0.008***
Macrocyclops albidus	--	--	--	--	--	--
Scapholeberis kingi	1.34	0.498	0.25	0.891	51.43	**0.008***
Unidentified calanoid	--	--	--	--	--	--
Unidentified cyclopoid	--	--	--	--	--	--
Calanoid copepodid	1.54	0.446	0.31	0.925	2.19	0.353
Cyclopoid copepodid	21.36	**0.008***	0.08	0.956	5.16	0.134

Note: boldface type and * denote significance at $\alpha = 0.05$; significance determined using residual (without replacement) resampling and a correlation matrix shrunk by 0.692 to account for correlation among response variables; univariate *P*-values adjusted for multiple univariate tests using the false discovery rate method; F = Fish Presence; T = Temperature; P = Species Pool; *Daphnia* spp. were analyzed as a single group; and *D. navus*, *M. albidus*, unidentified calanoids and unidentified cyclopoids were not included in analyses due to their limited occurrence, hence their values are replaced by dashes.

Table B-5.2 MANOVA table (part 2) summarizing the significance of treatment interaction effects on final taxa biomass.

	F x T		F x P		T x P		F x T x P	
Analysis	*F*	*P* (>F)	*F*	*P* (>F)	*F*	*P* (>F)	*F*	*P* (>F)
Full multivariate analysis	15.92	0.389	117.77	**0.001***	13.45	0.617	15.42	0.485
Arctodiaptomus arapahoensis	0.02	0.971	2.73	0.343	0.00	0.996	0.00	0.975
Acanthocyclops vernalis complex	1.78	0.446	11.10	**0.024***	0.21	0.917	1.10	0.607
Acanthodiaptomus denticornis	0.56	0.799	2.21	0.421	0.03	0.968	0.27	0.869
Aglaodiaptomus leptopus	2.56	0.390	0.38	0.869	0.21	0.925	2.00	0.434
Bosmina longirostris	0.09	0.941	18.85	**0.008***	0.09	0.941	0.42	0.828
Ceriodaphnia quadrangula	0.69	0.760	28.21	**0.008***	0.13	0.930	0.34	0.869
Chydorus sphaericus	0.02	0.971	23.53	**0.008***	0.01	0.974	0.34	0.869
Daphnia spp.	0.44	0.828	15.74	**0.008***	0.06	0.967	0.01	0.971
D. middendorffiana	--	--	--	--	--	--	--	--
D. pulex	--	--	--	--	--	--	--	--
D. mendotae	--	--	--	--	--	--	--	--
D. dentifera	--	--	--	--	--	--	--	--
D. unidentified	--	--	--	--	--	--	--	--
Diacyclops navus	--	--	--	--	--	--	--	--
Diacyclops thomasi	1.04	0.663	27.46	**0.008***	3.45	0.279	2.92	0.390
Diaphanosoma birgei	0.60	0.892	1.54	0.498	0.42	0.892	0.52	0.869
Eucyclops agilis	0.06	0.967	1.76	0.446	0.01	0.971	0.01	0.971
Hesperodiaptomus arcticus	0.11	0.939	9.46	**0.048***	0.01	0.971	0.01	0.971
Leptodiaptomus nudus	2.00	0.446	2.26	0.421	1.89	0.434	1.77	0.434
Leptodiaptomus sicilis	0.01	0.971	0.67	0.772	0.01	0.971	0.00	0.996
Leptodiaptomus tyrrelli	3.60	0.279	8.93	**0.042***	5.64	0.134	3.50	0.286
Macrocyclops albidus	--	--	--	--	--	--	--	--
Scapholeberis kingi	0.20	0.914	1.79	0.446	0.05	0.967	0.26	0.892
Unidentified calanoid	--	--	--	--	--	--	--	--
Unidentified cyclopoid	--	--	--	--	--	--	--	--
Calanoid copepodid	1.26	0.607	3.62	0.171	1.30	0.578	0.51	0.869
Cyclopoid copepodid	0.13	0.925	1.98	0.434	2.13	0.434	1.84	0.434

Note: boldface type and * denote significance at $\alpha = 0.05$; significance determined using residual (without replacement) resampling and a correlation matrix shrunk by 0.692 to account for correlation among response variables; univariate *P*-values adjusted for multiple univariate tests using the false discovery rate method; F = Fish Presence; T = Temperature; P = Species Pool; *Daphnia* spp. were analyzed as a single group; and *D. navus*, *M. albidus*, unidentified calanoids and unidentified cyclopoids were not included in analyses due to their limited occurrence, hence their values are denoted replaced by dashes.

Table B-5.3 RLQ summary statistics: eigenvalues (with percentage of total inertia projected in brackets) for the first two axes of the separate RLQ analyses (R for MCA of categorical treatments by tanks; L for CA of taxa biomass by tanks; and Q for PCA of mixed categorical and continuous traits by taxa) and the final RLQ; and RLQ axis covariance between R and Q and correlation with L (with percentage of optimal canonical correlation preserved in brackets).

Analysis and value	Axis 1	Axis 2
Preliminary ordinations		
R (treatments x tanks) eigenvalue	1.4557 (48.52%)	0.9925 (33.08%)
L (taxon biomass x tanks) eigenvalue	0.7057 (38.62%)	0.3772 (20.65%)
Q (traits x taxa) eigenvalue	1.7105 (57.02%)	1.1040 (36.80%)
RLQ ordination		
Eigenvalue	0.7986 (93.23%)	0.0576 (6.73%)
Covariance	0.8936	0.2400
Correlation	0.6757 (80.43%)	0.2422 (39.43%)

Table B-5.4 Results of fourth-corner analysis testing links between experimental factors and zooplankton functional traits.

Factor	Functional trait	Statistic	Obs	*P*
Fish presence	Motility	χ^2	24.2279	0.8893
	Feeding mode	χ^2	70.1992	0.6195
	Body size	Pseudo-*F*	940.5228	**0.0243***
Temperature	Motility	χ^2	10.2176	0.6195
	Feeding mode	χ^2	13.1595	0.6195
	Body size	Pseudo-*F*	1.8392	0.8893
Species pool	Motility	χ^2	1.3899	0.8893
	Feeding mode	χ^2	1.0804	0.8893
	Body size	Pseudo-*F*	354.9444	**0.0243***

Note: boldface type and * denote significance at $\alpha = 0.05$; significance determined using sequential randomization testing, by sites and taxa, using 49,999 permutations; and *P*-values adjusted for multiple univariate tests using the false discovery rate method.

Appendix C: Supplemental Information for Chapter 4

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Appendix C-3: Detailed statistical results

Table C-3.1 Total and unique proportions of variance in species composition attributable to individual environmental predictors (Model 3).

Group / Parameter	Total Adj R^2	Unique Adj R^2 Env Conditioned	Unique Adj R^2 Env + Spa Conditioned
Overall (n = 1,234)			
Annual Total Precipitation [a,b,c]	**0.0639 ***	**0.0093 ***	**0.0030 ***
Annual Mean Air Temperature [a,b,c]	**0.0612 ***	**0.0114 ***	**0.0028 ***
Mean Solar Radiation [a,b,c]	**0.0525 ***	**0.0081 ***	**0.0014 ***
Mixed Sedimentary Rock [a,b,c]	**0.0511 ***	**0.0023 ***	0.0002
Barren Land [a,b]	**0.0462 ***	**0.0025 ***	**0.0009 ***
Forest (Coniferous) [a,b]	**0.0444 ***	**0.0009 ***	**0.0006 ***
Non-Acidic Volcanics [a,b]	**0.0433 ***	**0.0025 ***	0.0003
Lake Perimeter [a,c]	**0.0393 ***	**0.0004 ‡**	**0.0004 ‡**
Forest (Mixedwood) [a,b,c]	**0.0392 ***	**0.0020 ***	**0.0009 ***
Lake Area [a,b,c]	**0.0389 ***	**0.0012 ***	**0.0010 ***
Grassland/Herbaceous [a,b,c]	**0.0364 ***	**0.0011 ***	0.0003
Catchment Area [a,b,c]	**0.0349 ***	**0.0006 ***	0.0003
Perennial Ice/Snow [a,b,c]	**0.0338 ***	**0.0016 ***	0.0003
Forest (Deciduous) [a,b,c]	**0.0313 ***	**0.0016 ***	**0.0006 ***
Wetlands (Emergent/Herbaceous) [a,b,c]	**0.0272 ***	**0.0017 ***	**0.0006 ***
Fish Introduction [a]	**0.0209 ***	**0.0037 ***	**0.0025 ***
Catchment Slope [b]	**0.0194 ***	---	---
Non-Carbonate Sedimentary Rock [a,b,c]	**0.0182 ***	**0.0006 ***	0.0003
Acidic Plutonics [a,b,c]	**0.0128 ***	**0.0040 ***	**0.0008 ***
Non-Acidic Plutonics [a,b,c]	**0.0123 ***	**0.0010 ***	**0.0004 ‡**
Shrub/Scrubland [a,b,c]	**0.0122 ***	**0.0009 ***	**0.0004 ‡**
Surface Water [a,b,c]	**0.0121 ***	**0.0015 ***	**0.0010 ***
Unconsolidated Sediment [a,b,c]	**0.0119 ***	**0.0031 ***	0.0002
Carbonate Sedimentary Rock [a,b,c]	**0.0115 ***	**0.0011 ***	**0.0004 ‡**
Wetlands (Wooded/Shrub) [a,b,c]	**0.0103 ***	**0.0012 ***	**0.0008 ***
Metamorphic Rock [a,b,c]	**0.0065 ***	**0.0024 ***	**0.0008 ***
Pyroclastics [c]	**0.0065 ***	---	---
Developed (Non-Vegetated) [a,b,c]	**0.0044 ***	**0.0007 ***	0.0003
Acidic Volcanics [a,b,c]	**0.0034 ***	**0.0011 ***	**0.0010 ***
Catchment Aspect [c]	**0.0014 ***	---	---
Evaporite [c]	**0.0008 ***	---	---
Agricultural [b,c]	**0.0007 ‡**	---	---
Asexual (n = 1,103)			
Annual Total Precipitation [a,b,c]	**0.0705 ***	**0.0149 ***	**0.0057 ***
Annual Mean Air Temperature [a,b,c]	**0.0581 ***	**0.0118 ***	**0.0042 ***
Mean Solar Radiation [a,b,c]	**0.0529 ***	**0.0064 ***	**0.0008 ‡**
Lake Perimeter [a,b,c]	**0.0513 ***	0.0001	0.0001
Lake Area [a,b,c]	**0.0511 ***	**0.0010 ‡**	**0.0007 ‡**

Group / Parameter	Total Adj R^2	Unique Adj R^2 Env Conditioned	Unique Adj R^2 Env + Spa Conditioned
Mixed Sedimentary Rock [a,b,c]	**0.0473 ***	**0.0017 ***	0 †
Catchment Area [a,b,c]	**0.0435 ***	**0.0010 ‡**	**0.0013 ***
Non-Acidic Volcanics [a,b]	**0.0424 ***	**0.0017 ***	0.0003
Forest (Coniferous) [a,b]	**0.0406 ***	**0.0018 ***	**0.0027 ***
Forest (Mixedwood) [a,b,c]	**0.0394 ***	**0.0027 ***	**0.0008 ‡**
Grassland/Herbaceous [c]	**0.0382 ***	---	---
Forest (Deciduous) [a,b,c]	**0.0371 ***	**0.0008 ‡**	0.0005
Barren Land [b]	**0.0313 ***	---	---
Perennial Ice/Snow [a,b,c]	**0.0290 ***	**0.0017 ***	0 †
Fish Introduction [a]	**0.0259 ***	**0.0059 ***	**0.0023 ***
Wetlands (Emergent/Herbaceous) [b,c]	**0.0255 ***	---	---
Non-Carbonate Sedimentary Rock [a,b,c]	**0.0235 ***	0.0006	0.0003
Surface Water [a,b,c]	**0.0184 ***	**0.0028 ***	**0.0015 ***
Non-Acidic Plutonics [a,b,c]	**0.0156 ***	**0.0018 ***	**0.0010 ***
Shrub/Scrubland [a,c]	**0.0153 ***	**0.0013 ***	**0.0009 ***
Acidic Plutonics [a,b,c]	**0.0128 ***	**0.0019 ***	0.0002
Carbonate Sedimentary Rock [a,b,c]	**0.0129 ***	0.0006	0.0003
Wetlands (Wooded/Shrub) [a,b,c]	**0.0123 ***	**0.0008 ‡**	0.0006
Pyroclastics [c]	**0.0082 ***	---	---
Unconsolidated Sediment [a,b,c]	**0.0079 ***	**0.0030 ***	0.0005
Metamorphic Rock [a,b,c]	**0.0076 ***	**0.0037 ***	**0.0008 ‡**
Catchment Slope [b]	**0.0075 ***	---	---
Acidic Volcanics [a,b,c]	**0.0042 ***	**0.0013 ***	**0.0018 ***
Developed (Non-Vegetated) [c]	**0.0029 ***	---	---
Catchment Aspect [c]	**0.0011 ‡**	---	---
Evaporite	**0.0005 ‡**	---	---
Agricultural	**0.0005 ‡**	---	---
Sexual (*n* = 1,155)			
Annual Total Precipitation [a,b,c]	**0.0672 ***	**0.0084 ***	**0.0019 ***
Mean Solar Radiation [a,b,c]	**0.0634 ***	**0.0113 ***	**0.0020 ***
Annual Mean Air Temperature [a,b,c]	**0.0633 ***	**0.0140 ***	**0.0019 ***
Mixed Sedimentary Rock [a,b,c]	**0.0566 ***	**0.0041 ***	**0.0005 ‡**
Barren Land [a,b]	**0.0519 ***	**0.0028 ***	**0.0022 ***
Non-Acidic Volcanics [a,b,c]	**0.0484 ***	**0.0040 ***	0 †
Forest (Mixedwood) [a,b,c]	**0.0469 ***	**0.0019 ***	**0.0017 ***
Forest (Coniferous)	**0.0411 ***	---	---
Lake Perimeter [c]	**0.0377 ***	---	---
Lake Area [a,b,c]	**0.0370 ***	**0.0023 ***	**0.0014 ***
Grassland/Herbaceous [a,b,c]	**0.0348 ***	**0.0026 ***	**0.0006 ‡**
Catchment Area [a,b,c]	**0.0348 ***	**0.0009 ***	0.0001
Forest (Deciduous) [a,b,c]	**0.0326 ***	**0.0028 ***	**0.0007 ‡**
Wetlands (Emergent/Herbaceous) [a,b,c]	**0.0321 ***	**0.0030 ***	**0.0010 ***
Perennial Ice/Snow [a,b,c]	**0.0314 ***	**0.0014 ***	**0.0010 ***
Catchment Slope [a,b]	**0.0280 ***	**0.0006 ‡**	0.0004
Fish Introduction [a]	**0.0176 ***	**0.0024 ***	**0.0031 ***

Group / Parameter	Total Adj R^2	Unique Adj R^2 Env Conditioned	Unique Adj R^2 Env + Spa Conditioned
Non-Carbonate Sedimentary Rock [b,c]	**0.0170 ***	---	---
Shrub/Scrubland [a,b]	**0.0162 ***	**0.0019 ***	**0.0009 ***
Unconsolidated Sediment [a,b,c]	**0.0155 ***	**0.0016 ***	0 †
Acidic Plutonics [a,b,c]	**0.0141 ***	**0.0041 ***	**0.0006 ‡**
Non-Acidic Plutonics [c]	**0.0131 ***	---	---
Wetlands (Wooded/Shrub) [a,b,c]	**0.0120 ***	**0.0021 ***	**0.0013 ***
Carbonate Sedimentary Rock [a,b,c]	**0.0114 ***	**0.0018 ***	0.0003
Surface Water [a,b,c]	**0.0098 ***	0.0005	0.0002
Metamorphic Rock [a,b,c]	**0.0080 ***	**0.0030 ***	**0.0012 ***
Pyroclastics [c]	**0.0065 ***	---	---
Developed (Non-Vegetated) [a,b,c]	**0.0049 ***	**0.0009 ***	0.0001
Acidic Volcanics [a,b,c]	**0.0038 ***	**0.0009 ***	**0.0006 ‡**
Catchment Aspect [c]	**0.0019 ***	---	---
Agricultural [b,c]	**0.0011 ***	---	---
Evaporite [c]	**0.0007 ‡**	---	---
Small (n = 1,142)			
Annual Total Precipitation [a,b,c]	**0.0662 ***	**0.0085 ***	**0.0034 ***
Mean Solar Radiation [a,b,c]	**0.0616 ***	**0.0108 ***	**0.0016 ***
Mixed Sedimentary Rock [a,b,c]	**0.0544 ***	**0.0026 ***	0 †
Lake Perimeter [b,c]	**0.0489 ***	---	---
Annual Mean Air Temperature [a,b,c]	**0.0488 ***	**0.0098 ***	**0.0032 ***
Lake Area [a,b,c]	**0.0485 ***	**0.0048 ***	**0.0014 ***
Non-Acidic Volcanics [a,b]	**0.0463 ***	**0.0038 ***	0.0001
Forest (Mixedwood) [a,b,c]	**0.0446 ***	**0.0017 ***	**0.0007 ‡**
Catchment Area [b,c]	**0.0425 ***	---	---
Grassland/Herbaceous [c]	**0.0400 ***	---	---
Forest (Deciduous) [a,b,c]	**0.0384 ***	**0.0015 ***	0.0002
Forest (Coniferous) [a,b]	**0.0352 ***	**0.0025 ***	**0.0021 ***
Barren Land [c]	**0.0300 ***	---	---
Perennial Ice/Snow [a,b,c]	**0.0265 ***	**0.0015 ***	0 †
Wetlands (Emergent/Herbaceous) [b,c]	**0.0255 ***	---	---
Fish Introduction [a]	**0.0217 ***	**0.0046 ***	**0.0018 ***
Non-Carbonate Sedimentary Rock [a,b,c]	**0.0211 ***	**0.0006 ‡**	**0.0005 ‡**
Non-Acidic Plutonics [a,b,c]	**0.0160 ***	**0.0017 ***	**0.0013 ***
Surface Water [a,b,c]	**0.0156 ***	**0.0024 ***	**0.0014 ***
Acidic Plutonics [a,b,c]	**0.0146 ***	**0.0040 ***	0.0003
Carbonate Sedimentary Rock [a,b,c]	**0.0146 ***	**0.0017 ***	0.0002
Shrub/Scrubland [a,b,c]	**0.0144 ***	**0.0013 ***	**0.0008 ‡**
Wetlands (Wooded/Shrub) [a,b,c]	**0.0144 ***	**0.0014 ***	**0.0010 ***
Unconsolidated Sediment [a,b,c]	**0.0120 ***	**0.0043 ***	0.0003
Catchment Slope [a,b]	**0.0101 ***	**0.0008 ‡**	**0.0007 ‡**
Pyroclastics [c]	**0.0078 ***	---	---
Metamorphic Rock [a,b,c]	**0.0072 ***	**0.0022 ***	**0.0013 ***
Developed (Non-Vegetated) [a,b,c]	**0.0052 ***	**0.0011 ***	**0.0006 ‡**
Acidic Volcanics [a,b,c]	**0.0031 ***	**0.0011 ***	**0.0011 ***

Group / Parameter	Total Adj R^2	Unique Adj R^2 Env Conditioned	Unique Adj R^2 Env + Spa Conditioned
Catchment Aspect ^{c}	**0.0011 ‡**	---	---
Agricultural ^{b,c}	**0.0007 ‡**	---	---
Evaporite	0.0004	---	---
Large (*n* = 1,014)			
Annual Mean Air Temperature ^{a,b,c}	**0.0859 ***	**0.0190 ***	**0.0041 ***
Annual Total Precipitation ^{a,b,c}	**0.0804 ***	**0.0142 ***	**0.0034 ***
Barren Land ^{a,b}	**0.0700 ***	**0.0039 ***	**0.0020 ***
Mean Solar Radiation ^{a,b,c}	**0.0627 ***	**0.0082 ***	**0.0023 ***
Mixed Sedimentary Rock ^{a,b,c}	**0.0586 ***	**0.0009 ‡**	0.0004
Forest (Coniferous)	**0.0579 ***	---	---
Forest (Mixedwood) ^{a,b,c}	**0.0516 ***	**0.0039 ***	**0.0011 ***
Non-Acidic Volcanics ^{a,b,c}	**0.0492 ***	**0.0032 ***	0.0005
Wetlands (Emergent/Herbaceous) ^{a,b,c}	**0.0403 ***	**0.0052 ***	**0.0026 ***
Perennial Ice/Snow ^{a,b,c}	**0.0398 ***	**0.0024 ***	**0.0015 ***
Catchment Slope ^{a,b}	**0.0391 ***	**0.0008 ‡**	**0.0007 ‡**
Lake Perimeter ^{c}	**0.0374 ***	---	---
Lake Area ^{a,b,c}	**0.0365 ***	**0.0010 ‡**	**0.0008 ‡**
Catchment Area ^{a,b,c}	**0.0360 ***	**0.0009 ‡**	0 †
Grassland/Herbaceous ^{a,b,c}	**0.0343 ***	**0.0017 ***	**0.0007 ‡**
Forest (Deciduous) ^{a,b,c}	**0.0307 ***	**0.0009 ‡**	**0.0011 ***
Fish Introduction ^{a}	**0.0229 ***	**0.0024 ***	**0.0025 ***
Non-Carbonate Sedimentary Rock ^{a,b,c}	**0.0209 ***	**0.0014 ***	**0.0010 ***
Shrub/Scrubland ^{a,b}	**0.0207 ***	**0.0023 ***	**0.0010 ***
Unconsolidated Sediment ^{a,b,c}	**0.0160 ***	**0.0025 ***	0.0002
Acidic Plutonics ^{a,b,c}	**0.0151 ***	**0.0058 ***	**0.0012 ***
Metamorphic Rock ^{a,b}	**0.0135 ***	**0.0073 ***	0.0004
Non-Acidic Plutonics ^{a,b,c}	**0.0122 ***	**0.0009 ‡**	**0.0006 ‡**
Carbonate Sedimentary Rock ^{b,c}	**0.0122 ***	---	---
Wetlands (Wooded/Shrub) ^{a,c}	**0.0106 ***	**0.0008 ‡**	**0.0007 ‡**
Surface Water ^{a,b,c}	**0.0099 ***	**0.0007 ‡**	**0.0007 ‡**
Pyroclastics ^{c}	**0.0071 ***	---	---
Acidic Volcanics ^{a,b,c}	**0.0055 ***	**0.0009 ‡**	0.0005
Developed (Non-Vegetated) ^{a,b,c}	**0.0028 ***	**0.0009 ‡**	0.0001
Catchment Aspect ^{b}	**0.0023 ***	---	---
Evaporite ^{c}	**0.0011 ***	---	---
Agricultural ^{b,c}	**0.0008 ‡**	---	---

Note: unique variation estimates (semipartials) were obtained conditioning by remaining variables from final selected environment (Env) and space (Spa) models; ^{a} denotes parameter was selected for inclusion in group full environment model; ^{b} denotes parameter was selected for inclusion in group climate or catchment/lake model; ^{c} denotes parameter natural log-transformed (parameters with non-detect values were log[x + (0.5·lowest detected value)]-transformed); boldface type and * denotes parameter estimate P ≤0.01 as determined by permutation testing with 100,000 iterations; boldface type and ‡ denotes parameter estimate P <0.05 and >0.01 as determined by permutation testing with 100,000 iterations; and † denotes adjusted R^2 <0.00005.

Table C-3.2 Total, unique, and shared proportions of variance in species composition attributable to environment, space, and geography explanatory matrices (Model 1).

Fraction	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Env	27	**0.2286** *	23	**0.2140** *	24	**0.2605** *	23	**0.2201** *	25	**0.3046** *
Total Spa	53	**0.2473** *	32	**0.2234** *	53	**0.3015** *	33	**0.2414** *	46	**0.3348** *
Total Geo	3	**0.1587** *	3	**0.1427** *	3	**0.1896** *	3	**0.1641** *	3	**0.1954** *
[a] Unique Env	27	**0.0324** *	23	**0.0353** *	24	**0.0317** *	23	**0.0295** *	25	**0.0427** *
[b] Unique Spa	53	**0.0540** *	32	**0.0466** *	53	**0.0715** *	33	**0.0440** *	46	**0.0821** *
[c] Unique Geo	3	**0.0028** *	3	**0.0020** *	3	**0.0039** *	3	**0.0038** *	3	**0.0028** *
[d] Env + Spa	0	0.0527	0	0.0491	0	0.0596	0	0.0462	0	0.0833
[e] Spa + Geo	0	0.0124	0	0.0111	0	0.0165	0	0.0159	0	0.0141
[f] Env + Geo	0	0.0154	0	0.0129	0	0.0153	0	0.0091	0	0.0232
[g] Env + Spa + Geo	0	0.1281	0	0.1167	0	0.1540	0	0.1354	0	0.1554
Residual	0	0.7022	0	0.7264	0	0.6477	0	0.7162	0	0.5965

Note: boldface type and * denotes parameter estimate $P \leq 0.01$ as determined by permutation testing with 100,000 iterations; and Env, Spa, and Geo refer environment, space, and geography, respectively.

Table C-3.3 Total, unique, and shared proportions of variance in species composition attributable to climate, catchment/lake, fish introduction, and space explanatory matrices (Model 2).

Fraction	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Cli	3	**0.1371** *	3	**0.1341** *	3	**0.1593** *	3	**0.1283** *	3	**0.1973** *
Total Cat	24	**0.1891** *	21	**0.1770** *	22	**0.2140** *	23	**0.1828** *	23	**0.2538** *
Total Fis	1	**0.0209** *	1	**0.0259** *	1	**0.0176** *	1	**0.0217** *	1	**0.0229** *
Total Spa	53	**0.2473** *	32	**0.2234** *	53	**0.3015** *	33	**0.2414** *	46	**0.3348** *
[a] Unique Cli	3	**0.0071** *	3	**0.0087** *	3	**0.0060** *	3	**0.0071** *	3	**0.0096** *
[b] Unique Cat	24	**0.0234** *	21	**0.0210** *	22	**0.0252** *	23	**0.0191** *	23	**0.0335** *
[c] Unique Fis	1	**0.0025** *	1	**0.0023** *	1	**0.0031** *	1	**0.0017** *	1	**0.0025** *
[d] Unique Spa	53	**0.0668** *	32	**0.0569** *	53	**0.0876** *	33	**0.0594** *	46	**0.0967** *
[e] Cli + Cat	0	0.0106	0	0.0098	0	0.0097	0	0.0059	0	0.0181
[f] Cat + Fis	0	0.0022	0	0.0038	0	0.0009	0	0.0040	0	0.0008
[g] Cli + Fis	0	0.0002	0	0.0002	0	0.0001	0	0.0002	0	0.0003
[h] Cli + Spa	0	0.0253	0	0.0196	0	0.0347	0	0.0236	0	0.0360

Fraction	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
[i] Cat + Spa	0	0.0611	0	0.0485	0	0.0725	0	0.0644	0	0.0711
[j] Fis + Spa	0	0.0012	0	0.0034	0	0 †	0	0.0027	0	0 †
[k] Cli + Cat + Spa	0	0.0803	0	0.0807	0	0.0954	0	0.0793	0	0.1137
[l] Cli + Cat + Fis	0	0.0022	0	0.0019	0	0.0021	0	0.0011	0	0.0019
[m] Cat + Fis + Spa	0	0.0011	0	0.0011	0	0.0008	0	0.0008	0	0 †
[n] Cli + Fis + Spa	0	0.0033	0	0.0031	0	0.0038	0	0.0031	0	0.0030
[o] Cli + Cat + Fis + Spa	0	0.0082	0	0.0102	0	0.0074	0	0.0081	0	0.0145
Residual	0	0.7046	0	0.7290	0	0.6513	0	0.7195	0	0.5983

Note: boldface type and * denotes parameter estimate $P \leq 0.01$ as determined by permutation testing with 100,000 iterations; † denotes adjusted R^2 <0.00005; and Cli, Cat, Fis, and Spa refer to components of variation attributable to climate, catchment/lake, fish introduction, and space, respectively.

Table C-3.4 Total, unique, and shared proportions of variance in species composition attributable to environment, space, and connectivity explanatory matrices (Model 4).

	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Env	27	**0.2286** *	23	**0.2140** *	24	**0.2605** *	23	**0.2201** *	27	**0.3046** *
Total Spa	53	**0.2473** *	32	**0.2234** *	53	**0.3015** *	33	**0.2414** *	46	**0.3348** *
Total Con	1	**0.1699** *	1	**0.1366** *	1	**0.2216** *	1	**0.1722** *	1	**0.2409** *
[a] Unique Env	27	**0.0450** *	23	**0.0474** *	24	**0.0413** *	23	**0.0372** *	27	**0.0595** *
[b] Unique Spa	53	**0.0506** *	32	**0.0469** *	53	**0.0610** *	33	**0.0457** *	46	**0.0648** *
[c] Unique Con	1	**0.0057** *	1	**0.0050** *	1	**0.0070** *	1	**0.0071** *	1	**0.0060** *
[d] Env + Spa	0	0.0353	0	0.0456	0	0.0315	0	0.0320	0	0.0415
[e] Spa + Con	0	0.0159	0	0.0107	0	0.0269	0	0.0142	0	0.0313
[f] Env + Con	0	0.0028	0	0.0009	0	0.0056	0	0.0014	0	0.0064
[g] Env + Spa + Con	0	0.1455	0	0.1201	0	0.1821	0	0.1496	0	0.1972
Residual	0	0.6992	0	0.7234	0	0.6445	0	0.7130	0	0.5932

Note: boldface type and * denotes parameter estimate $P \leq 0.01$ as determined by permutation testing; Env, Spa, and Con refer to components of variation attributable to environment, space, and connectivity, respectively; and connectivity α constant for overall community = 104,467, asexual species = 69,645, sexual species = 104,467, small species = 104,467, and large species = 69,645.

Appendix C-4: Sensitivity analyses

As a quantitative synthesis of multiple historical data sources, there exists potential for the results to reflect biases among individual sampling locations or studies. To evaluate the extent to which my interpretations may be confounded by variations in sampling effort (i.e. number of sampling years integrated for species occurrence estimates), sampling year (i.e. most recent confirmed date when multiple samples were taken), or data source (i.e. research group or taxonomist) I conducted a series of sensitivity analyses (Tables C-4.1–C-4.3).

Results of the sensitivity analyses suggest that my findings are robust and support my interpretations. Differences in sampling effort and sampling year explain much less total species variance than environment, space, or geography (Tables C-4.1 & C-4.2). Further, sampling effort and sampling year each uniquely explain less than 0.5 % of total species variance and impart a negligible influence on the unique contributions of environmental and spatial predictors. These results suggest that unique variation attributed to sampling effort and sampling year is mostly linked to the unexplained residual fraction of species variance, and does not influence my interpretation of spatial or environmental factors. Conversely, data source explains a much larger amount of total variance, which covaries with space, geography, and spatially structured environmental variables (Table C-4.3). This result was expected, as different research groups generally collect data at different geographic locations characterized by different spatially structured environmental conditions. Critically though, the ranking of environmental and spatial structures was unaffected by data source, indicating that my interpretations are robust.

Table C-4.1 Total, unique, and shared proportions of variance in species composition attributable to environment, space, geography, and sampling effort matrices.

	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Env	27	**0.2286** *	23	**0.2140** *	24	**0.2605***	23	**0.2201** *	25	**0.3046** *
Total Spa	53	**0.2473** *	32	**0.2234** *	53	**0.3015***	33	**0.2414** *	46	**0.3348** *
Total Geo	3	**0.1587** *	3	**0.1427** *	3	**0.1896***	3	**0.1641** *	3	**0.1954** *
Total Eff	1	**0.0074** *	1	**0.0063** *	1	**0.0096***	1	**0.0080** *	1	**0.0081** *
[a] Unique Env	27	**0.0322** *	23	**0.0353** *	24	**0.0313***	23	**0.0298** *	25	**0.0418** *
[b] Unique Spa	53	**0.0539** *	32	**0.0468** *	53	**0.0713***	33	**0.0440** *	46	**0.0818** *
[c] Unique Geo	3	**0.0026** *	3	**0.0019** *	3	**0.0036***	3	**0.0037** *	3	**0.0025** *
[d] Unique Eff	1	**0.0022** *	1	**0.0025** *	1	**0.0012***	1	**0.0026** *	1	**0.0015** *

	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
[e] Env + Spa	0	0.0527	0	0.0493	0	0.0595	0	0.0463	0	0.0830
[f] Spa + Geo	0	0.0124	0	0.0111	0	0.0161	0	0.0159	0	0.0141
[g] Env + Geo	0	0.0147	0	0.0125	0	0.0150	0	0.0084	0	0.0228
[h] Env + Eff	0	0.0001	0	0 †	0	0.0004	0	0 †	0	0.0009
[i] Spa + Eff	0	0.0002	0	0 †	0	0.0002	0	0 †	0	0.0003
[j] Geo + Eff	0	0.0002	0	0 †	0	0.0003	0	0.0001	0	0.0003
[k] Env + Spa + Eff	0	0.0001	0	0 †	0	0.0002	0	0 †	0	0.0002
[l] Env + Spa + Geo	0	0.1243	0	0.1130	0	0.1472	0	0.1302	0	0.1510
[m] Spa + Geo + Eff	0	0 †	0	0 †	0	0.0004	0	0 †	0	0 †
[n] Env + Geo + Eff	0	0.0007	0	0.0004	0	0.0003	0	0.0007	0	0.0005
[o] Env + Spa + Geo + Eff	0	0.0038	0	0.0036	0	0.0068	0	0.0052	0	0.0045
Residual	0	0.6999	0	0.7238	0	0.6464	0	0.7136	0	0.5949

Note: boldface type and * denotes parameter estimate $P \leq 0.01$ as determined by permutation testing with 100,000 iterations; † denotes adjusted $R^2 < 0.00005$; sampling effort is the number of sampling years integrated for species occurrence estimates at each sampling location; and Env, Spa, Geo, and Eff refer to components of variation attributable to environment, space, geography, and sampling effort, respectively.

Table C-4.2 Total, unique, and shared proportions of variance in species composition attributable to environment, space, geography, and sampling year explanatory matrices.

	Overall (n = 1,127)		Asexual (*n* = 1,020)		Sexual (*n* = 1,059)		Small (*n* = 1,060)		Large (*n* = 928)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Env	27	**0.2319** *	23	**0.2172** *	24	**0.2647** *	23	**0.2242** *	25	**0.3094** *
Total Spa	53	**0.2512** *	32	**0.2286** *	53	**0.3044** *	33	**0.2479** *	46	**0.3368** *
Total Geo	3	**0.1702** *	3	**0.1550** *	3	**0.2004** *	3	**0.1772** *	3	**0.2026** *
Total Yea	1	**0.0348** *	1	**0.0361** *	1	**0.0328** *	1	**0.0458** *	1	**0.0210** *
[a] Unique Env	27	**0.0280** *	23	**0.0332** *	24	**0.0283** *	23	**0.0268** *	25	**0.0381** *
[b] Unique Spa	53	**0.0535** *	32	**0.0481** *	53	**0.0690** *	33	**0.0448** *	46	**0.0793** *
[c] Unique Geo	3	**0.0026** *	3	**0.0018** *	3	**0.0037** *	3	**0.0031** *	3	**0.0027** *
[d] Unique Yea	1	**0.0026** *	1	**0.0048** *	1	**0.0012** *	1	**0.0026** *	1	**0.0021** *
[e] Env + Spa	0	0.0421	0	0.0400	0	0.0484	0	0.0330	0	0.0767
[f] Spa + Geo	0	0.0085	0	0.0091	0	0.0124	0	0.0113	0	0.0107
[g] Env + Geo	0	0.0160	0	0.0141	0	0.0153	0	0.0091	0	0.0240
[h] Env + Yea	0	0.0012	0	0.0005	0	0.0011	0	0.0013	0	0.0022
[i] Spa + Yer	0	0.0009	0	0 †	0	0.0020	0	0.0017	0	0.0019
[j] Geo + Yea	0	0.0005	0	0.0006	0	0.0008	0	0.0008	0	0.0006
[k] Env + Spa + Yea	0	0.0028	0	0.0003	0	0.0038	0	0.0030	0	0.0026
[l] Env + Spa + Geo	0	0.1157	0	0.0993	0	0.1443	0	0.1164	0	0.1530

	Overall (n = 1,127)		Asexual (*n* = 1,020)		Sexual (*n* = 1,059)		Small (*n* = 1,060)		Large (*n* = 928)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
[m] Spa + Geo + Yea	0	0.0008	0	0.0003	0	0.0004	0	0.0019	0	0 †
[n] Env + Geo + Yea	0	0 †	0	0 †	0	0 †	0	0 †	0	0 †
[o] Env + Spa + Geo + Yea	0	0.0270	0	0.0317	0	0.0242	0	0.0358	0	0.0140
Residual	0	0.6987	0	0.7184	0	0.6459	0	0.7096	0	0.5946

Note: * denotes parameter estimate *P* ≤0.01 as determined by permutation testing with 100,000 iterations; † denotes adjusted R^2 <0.00005; sampling year is the most recent confirmed sampling year at each sampling location; locations with uncertain sampling dates were excluded from analysis (*n* = 107); and Env, Spa, Geo, and Yea refer to components of variation attributable to environment, space, geography, and sampling year, respectively.

Table C-4.3 Total, unique, and shared proportions of variance in species composition attributable to environment, space, geography, and data source explanatory matrices.

	Overall (n = 1,234)		Asexual (*n* = 1,103)		Sexual (*n* = 1,155)		Small (*n* = 1,142)		Large (*n* = 1,014)	
Fraction	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2	df	Adj R^2
Total Env	27	**0.2286 ***	23	**0.2140 ***	24	**0.2605 ***	23	**0.2201 ***	25	**0.3046 ***
Total Spa	53	**0.2473 ***	32	**0.2234 ***	53	**0.3015 ***	33	**0.2414 ***	46	**0.3349 ***
Total Geo	3	**0.1587 ***	3	**0.1427 ***	3	**0.1896 ***	3	**0.1641 ***	3	**0.1954 ***
Total Dat	15	**0.1877 ***	15	**0.1911 ***	15	**0.2075 ***	15	**0.2071 ***	14	**0.2119 ***
[a] Unique Env	27	**0.0254 ***	23	**0.0305 ***	24	**0.0230 ***	23	**0.0227 ***	25	**0.0354 ***
[b] Unique Spa	53	**0.0369 ***	32	**0.0341 ***	53	**0.0497 ***	33	**0.0251 ***	46	**0.0617 ***
[c] Unique Geo	3	**0.0016 ***	3	0.0008	3	**0.0018 ***	3	**0.0017 ***	3	**0.0023 ***
[d] Unique Dat	15	**0.0173 ***	15	**0.0224 ***	**15**	**0.0209 ***	**15**	**0.0192 ***	**14**	**0.0155 ***
[e] Env + Spa	0	0.0209	0	0.0153	0	0.0265	0	0.0161	0	0.0309
[f] Spa + Geo	0	0.0019	0	0.0018	0	0.0043	0	0.0018	0	0.0080
[g] Env + Geo	0	0.0156	0	0.0115	0	0.0161	0	0.0089	0	0.0247
[h] Env + Dat	0	0.0070	0	0.0048	0	0.0087	0	0.0068	0	0.0074
[i] Spa + Dat	0	0.0171	0	0.0125	0	0.0218	0	0.0189	0	0.0204
[j] Geo + Dat	0	0.0012	0	0.0012	0	0.0020	0	0.0021	0	0.0005
[k] Env + Spa + Dat	0	0.0319	0	0.0338	0	0.0332	0	0.0301	0	0.0524
[l] Env + Spa + Geo	0	0.0251	0	0.0109	0	0.0443	0	0.0197	0	0.0444
[m] Spa + Geo + Dat	0	0.0105	0	0.0093	0	0.0122	0	0.0140	0	0.0061
[n] Env + Geo + Dat	0	0 †	0	0.0015	0	0 †	0	0.0002	0	0 †
[o] Env + Spa + Geo + Dat	0	0.1030	0	0.1058	0	0.1097	0	0.1157	0	0.1111
Residual	0	0.6849	0	0.7040	0	0.6268	0	0.6970	0	0.5809

Note: boldface type and * denotes parameter estimate *P* ≤0.01 as determined by permutation testing with 100,000 iterations; † denotes adjusted R^2 <0.00005; data sources are the taxonomist or research group/lab responsible for zooplankton records at each sampling location, and were represented by a set of dummy variables; and Env, Spa, Geo, and Dat refer to components of variation attributable to environment, space, geography, and data source, respectively.