IMPACTS OF ANTHROPOGENIC ENVIRONMENTAL CHANGES ON BIODIVERSITY, ECOSYSTEM PROCESSES, AND TROPHIC INTERACTIONS

by

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This thesis is dedicated to my parents for fostering my love of nature through hundreds of nights spent camping under the stars

Table Of Contents

List Of Tables

List Of Figures

Abstract

Habitat loss, climate change, invasive species, nitrogen deposition, and over-exploitation are all contributing to a global biodiversity crisis. Yet, there is high uncertainty in regards to which drivers exert the largest influence on local biodiversity and ecosystem processes, and how the magnitude, direction, and consistency of responses compares across drivers, habitats, and trophic groups. In this thesis, I generated worldwide databases of empirically derived ecosystem responses to global change and evaluated general trends in local biodiversity and ecosystem responses to several human-induced environmental changes. I then used projections of future environmental change across the Earth's biomes to assess biases in the spatial distribution of local biodiversity change studies. Lastly, My results revealed widespread decline in local species richness from human-induced environmental changes by an average 18%. Species loss was greatest following land-use change and species invasions. In contrast, species invasions had little consistent impact on several ecosystem processes, and instead warming was the major driver of ecosystem function change. I also observed strong, yet opposite, trends in the predictability of biodiversity responses for species invasions and removals, suggesting that accuracy in forecasting community change is dependent on habitat and trophic role. My analyses emphasized that the biodiversity data used in current biodiversity change syntheses is not geographically representative and I provide recommendations for where future studies should be conducted. Finally, my experiments revealed a strong impact of warming on top predators that cascaded to lower trophic levels. This demonstrates how ecosystem responses to global change are influenced by trophic structure and shows that indirect effects mediated by species interactions can be equally important as direct effects of global change drivers in restructuring ecological communities.

My thesis represents a comprehensive empirical evaluation of how contemporary ecosystems respond to human-induced environmental changes. I have illustrated several general trends of local biodiversity and ecosystem process responses across drivers, habitats, biomes, and trophic groups that may inform future predictive analyses of how global change impacts ecosystems around the globe.

List Of Abbreviations Used

ANOVA	Analysis of variance
Chl	Chlorophyll
CI	Confidence interval
e	Euler's number (base of natural logarithm)
ES	Effect size
n_c	Sample size—control condition
n_i	Sample size—impacted condition
PERMANOVA	Permutation-based analysis of variance
PRISMA	Preferred reporting items for systematic reviews and meta-analyses
RR	Response ratio
RP	Response predictability
S_c	Standard deviation—control condition
S_i	Standard deviation—impacted condition
SE	Standard error
SD	Standard deviation
SEM	Structural equation model
SR	Species richness
Q	Heterogeneity statistic
Q_t	Total heterogeneity
Q_w	Within-group heterogeneity
Q_b	Between-group heterogeneity
Q_m	Model heterogeneity
$\overline{X}_c$	Average—control condition
$\overline{X}_i$	Average—impacted condition

Acknowledgments

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CHAPTER 1

INTRODUCTION

1.1   General Introduction

Anthropogenic global change is altering ecosystems at an unprecedented rate through numerous environmental changes, including, *inter alia,* habitat loss and land transformation, spread of non-native species, increased temperatures, nitrogen deposition, over-exploitation, and acidification (Vitousek et al. 1997). These human-induced environmental changes are impacting ecosystems worldwide, resulting in shifts in species abundances and biotic interactions that ultimately alter biodiversity and community structure (Dawson et al. 2011; Worm & Paine 2016). Understanding how different global change scenarios reorganize ecosystems has become one of the most relevant areas of ecological inquiry. Yet the vast majority of studies that examine ecosystem responses to global change focus on the impacts of just one or two drivers. Thus, globally, it remains unclear which drivers exert the largest influence on local biodiversity and ecosystem processes, how the magnitude, direction, and consistency of responses compares across drivers, habitats, biomes, and trophic groups, and whether there exists generalizable ecosystem responses to human-driven environmental changes.

The non-random nature of species loss in human influenced communities is well recognized and results from a disproportional vulnerability of species to global change drivers (Zavaleta et al. 2009). Species vulnerability depends on both species traits (e.g. trophic position) and specific driver characteristics (e.g. abiotic vs. biotic perturbation), and differences in vulnerability suggest that the nature and extent of ecosystem responses to drivers will vary. For example, drivers that result in immediate biotic restructuring (e.g. species invasions and removals) are expected to have higher magnitude responses relative

to drivers that initially impact physiological processes (e.g. warming, nutrient addition, acidification) (Smith et al. 2015). Drivers that disproportionately impact high trophic position species, such as habitat transformation (Gonzalez et al. 2011; Bartlett et al. 2016) and warming (Petchey et al. 1999; Vasseur & McCann 2005), may produce cascading trophic interactions that result in greater ecosystem responses relative to drivers whose effects are more localized. Ecosystems also exhibit a range of sensitivities to global change drivers, which may be related to food web structure and strength of species interactions (Shurin et al. 2002; Rooney et al. 2006) and the natural variability of drivers in each ecosystem (Flombaum et al. 2016). Furthermore, there is considerable uncertainty regarding how patterns of global biodiversity play out across scales (McGill et al. 2015). Several studies have shown that, while global biodiversity is declining, local biodiversity can remain the same (Vellend et al. 2013; Dornelas et al. 2014) or increase (Sax & Gaines 2003; Elahi et al. 2015).

The average trends of local biodiversity change remain unclear (Gonzalez et al. 2016), and a comprehensive evaluation of the magnitude and direction of local human-induced biodiversity change across the globe is necessary to provide an accurate assessment. The aim of this thesis is to evaluate general trends in local biodiversity and ecosystem responses to human-induced environmental changes and examine the role that altered species interactions play in mediating the community-level responses to global change.

1.2   Research Approach

A rapidly growing number of empirical studies are being conducted to gain insight into how human-induced environmental changes alter ecological communities. However, there has never been a quantitative assessment to characterize and compare the biodiversity and ecosystem responses to human-induced environmental change across globally distributed empirical data to determine general patterns of ecosystem change in response to human activities. In this thesis I use a series of meta-analyses to assess the magnitude, direction, and consistency of biodiversity and ecosystem process responses across drivers, habitats, biomes, and trophic groups. Along with identifying general trends of local ecosystem responses to global change, I conduct a case study using a multi-

trophic aquatic model ecosystem to more closely examine the underlying mechanisms that lead to community change.

There is growing recognition of the critical role that biotic interactions play in driving biodiversity and ecosystem processes, and the necessity of exploring how the nature and strength of species interactions are influenced by environmental stressors to better understand the community-level effects of anthropogenic global change (Poisot et al. 2012; McCann 2007). Furthermore, the indirect effects of environmental change that are driven by species interactions are potentially as, or more, important than direct effects in shaping communities (Kordas et al. 2011; Shurin et al. 2012; Alsterberg et al. 2013). Yet, the relative strengths of indirect and direct effects are not typically considered in global change experiments despite their importance in predicting the ecosystem impacts of global change (Smith et al. 2009; Wernberg et al. 2012; Harvey et al. 2016). Therefore, I use laboratory analogs of natural rock pool communities as a model ecosystem to test the community responses to warming and acidification and more closely examine how these drivers mediate community change through direct and indirect effects. Rock pools are multi-trophic aquatic habitats that are found along rocky coastlines around the world and contain a diverse suite of algae, meiofauna, and zooplankton. Their small size, contained structure, and ability to support a persistent and complete ecological community make them ideal model ecosystems for global change experiments (Srivastava et al. 2004; Benton et al. 2007).

1.3   Thesis Outline

This thesis is presented in a publication-based format. All manuscripts have been published (Chapters 2, 3, and 4), currently in peer-review (Chapter 6), or are in preparation for submission (Chapter 5) to peer-reviewed scientific journals. Publication details are provided on the first page of each chapter. The publication licenses for all published chapters permit the reproduction of published articles without the requirement of copyright permission. The references for each chapter are compiled into a single reference list, which is provided after Chapter 7. Following this introduction, my thesis is organized into 5 manuscript chapters:

Chapter 2 (*Local biodiversity loss from human-induced environmental changes*) quantifies and compares the local-scale biodiversity response to five of the most pervasive global change drivers impacting ecosystems today. In this chapter I compiled a global database of 245 published studies and analyzed the magnitude of change in local species richness among drivers, habitats, and trophic roles. My results reveal widespread local biodiversity loss following human-induced environmental change, particularly for land use change and species invasions, and contrast other recently published syntheses that suggest local biodiversity is not declining.

Chapter 3 (*Data gaps in local biodiversity change studies across the Earth's terrestrial biomes*) assesses the biases that exist in the spatial distribution of local biodiversity change studies. I compiled a database of 767 published studies and analyzed how well biodiversity change studies are represented across terrestrial biomes based on: (1) the land area of each biome, (2) the future change in human activities projected for each biome, (3) and the impact of human activities on each biomes biodiversity. In this chapter I provide recommendations for where future biodiversity monitoring efforts should be focused to gain a more representative sample of how human activities are changing terrestrial biodiversity across the globe.

Chapter 4 (*Predictability of community responses to human-induced environmental changes*) considers how global change drivers impact the predictability of biodiversity responses by analyzing the within-replicate variability of 91 global change experiments, as opposed to the more commonly evaluated metric, the average value of biodiversity change. My results show that species removals lead to highly variable biodiversity responses, while species invasions lead to increased predictability. This chapter demonstrates that, in contrast to the clear negative effect of global change drivers on average biodiversity (as shown in Chapter 2), the consistency of the biodiversity response is highly contingent on the specific type of human-induced environmental change and whether species are being added to, or lost from, the community.

Chapter 5 (*Impacts of human-induced environmental changes on ecosystem processes*) explores the extent to which five drivers of global change impact ecosystem functioning. I compiled a global database of 270 published studies to determine if the main drivers of local biodiversity change that I identified in Chapter 2 also contribute to large changes in

key ecosystem processes. In contrast to the effects on biodiversity, my results show that species invasions, on average, have no significant impact on the magnitude of change for several ecosystem processes. Instead, warming and nitrogen deposition were identified as the major drivers of change in key ecosystem processes.

Chapter 6 (*Cascading effects of climate change on plankton community structure*) disentangles the direct and indirect effects of two prominent human-induced environmental changes (climate warming and acidification) on plankton community structure. Using a combination of factorial experiments and meta-analyses I show how warming and acidification not only result in direct impacts on plankton species at the top and bottom of food webs, but also alter trophic interactions that cascade through the entire plankton community. This chapter emphasizes that cascading trophic interactions can be just as important as the direct effects of human-driven environmental change in restructuring ecological assemblages.

The seventh and final chapter of this thesis integrates the conclusions from each of my chapters to synthesize my findings, to discuss the contributions that my doctoral research has made to the study of biodiversity change and global change ecology, and to identify future research directions.

CHAPTER 2

LOCAL BIODIVERSITY LOSS FROM HUMAN-INDUCED ENVIRONMENTAL CHANGES

The work presented in Chapter 2 also appears in:

Murphy GEP, Romanuk TN (2014) A meta-analysis of declines in local species richness from human disturbances. Ecology and Evolution 4:91-103.

2.1   Abstract

There is high uncertainty surrounding the magnitude of current and future biodiversity change that is occurring due to human-induced environmental change. Here we present a globally spanning meta-analysis of aquatic and terrestrial empirical studies that report 327 measures of change in local species richness from five major drivers of global change. On average, global change drivers lead to an 18.3% decline in species richness. Declines in species richness were highest for endotherms (33.2%), followed by producers (25.1%), and ectotherms (10.5%). Land-use change and species invasions had the largest impact on species richness resulting in a 24.8% and 23.7% decline, respectively, followed by habitat loss (14%), nutrient addition (8.2%), and increases in temperature (3.6%). Across all drivers of change, declines in species richness were greater for terrestrial biomes (22.4%) than aquatic biomes (5.9%). In the tropics, habitat loss and land-use change had the largest impact on species richness whereas in the boreal forest and northern temperate forests species invasions had the largest impact on species richness. Along with revealing general trends in the biodiversity responses to global change drivers across different drivers, biomes, and taxa, our results also identify critical knowledge gaps for predicting the effects of global change drivers on Earth's biomes.

2.2 Introduction

Developing the ability to predict the consequences of environmental change is one of the most significant challenges in ecology today (Chapin et al. 1997; Pereira et al. 2010a; Dawson et al. 2011). Evidence is increasingly demonstrating the negative effects of biodiversity loss on Earth's ecosystem processes (Loreau et al. 2001; Balvanera et al. 2006; Wardle et al. 2011; Hooper et al. 2012). Given the increasing human domination of Earth's biomes, establishing accurate estimates of the magnitude of biodiversity loss resulting from common human drivers of change, such as land-use alterations and habitat loss, species invasions, climate change, and nutrient addition, is of particular importance.

With the sustainability of human life on Earth relying on the services that healthy ecosystems provide (MA 2005), a better understanding of why and how species are being lost from ecosystems is needed. There is considerable uncertainly however over the magnitude of current and future biodiversity loss (Barnosky et al. 2012). Previous attempts to estimate changes in biodiversity have relied heavily on expert opinion (Sala et al. 2000) or have focused on estimating extinction risks for particular taxa (Thuiller et al. 2005). Potential time lags between environmental change and extinctions (Krauss et al. 2010), differences in extinction rate estimates based on species-area-curves (He & Hubbell 2011), and other confounding effects have made predicting the magnitude of species loss resulting from various human-induced environmental changes problematic (Bellard et al. 2012). Differences between modeling approaches and uncertainties within model projections have also resulted in widely varying predictions of future biodiversity change (Peireria et al. 2010). For example, two modeling approaches used to project the future global extinction risks for birds revealed very different estimates with Jetz et al. (2007) projecting 253-455 species at risk for extinction by the year 2100 while Sekercioglu et al. (2008) projects 2150 species at risk for extinction in the same time period.

One potential solution for the uncertainties in estimating biodiversity change is making use of empirical studies that report the difference in species richness between reference and human influenced habitats. Species richness is not synonymous with biodiversity, with the later serving as a more complex description of both the variation in the number of species and their relative abundances, along with genetic and ecosystem

variation. However, declines in species richness can be an indicator of biodiversity loss, and with studies that examine changes in species richness following global change drivers amongst the most common in the ecological literature, compiling these studies and analyzing their responses can provide information on the potential biodiversity loss occurring from human-induced environmental changes. In this paper, we have compiled studies that document the effects of human-induced environmental changes on species richness into a dataset that includes 327 empirical values of change in species richness taken from 245 previously published experimental and observational studies. Using a combination of categorical and continuous meta-analyses we determined whether there are differences in the magnitude of species richness responses resulting from five global change drivers: species invasions, nutrient addition, temperature increase, habitat loss or fragmentation, and land-use change. We also determined if the species richness response to global change drivers differed based on: 1) the type of biome (Northern temperate forest, boreal forest, tropical, or aquatic), 2) the type of species (producer, ectotherm, or endotherm), 3) the type of study (experimental or observational), 4) the initial species richness, 5) the latitude of the study site, and 6) the length of the experiment.

2.3   Methods

2.3.1 Selection Criteria

Our dataset was compiled by searching the biological literature for studies that reported the effects of anthropogenic global change drivers on species richness. We focused on five human-induced environmental changes that have been identified as major drivers of current biodiversity decline: species invasions, nutrient addition, temperature increase, habitat loss or fragmentation, and land-use change (Vitousek et al. 1997; Jackson et al. 2001). We performed a literature search using the ISI Web of Science database of the following research areas: 'environmental sciences ecology', 'biodiversity conservation', and 'marine freshwater biology'. We used the following search expressions: "biodiversity loss" OR "species loss" OR "species richness" OR "community change" AND ("invasi* species" OR "habitat loss" OR "land use change" OR "climate change" OR "experiment* warm*" OR increas* temperature" OR "eutrophication" OR "nutrient

add*"). A final search of the literature was completed on 10 February 2013. We searched for studies that experimentally manipulated drivers (n=113) or observational studies that compared an impacted (treatment) habitat with a reference (control) habitat (n=214). The literature search yielded 114,597 citations, of which 245 studies that included 327 values of change in species richness were included in the final dataset (Figure 2.1).
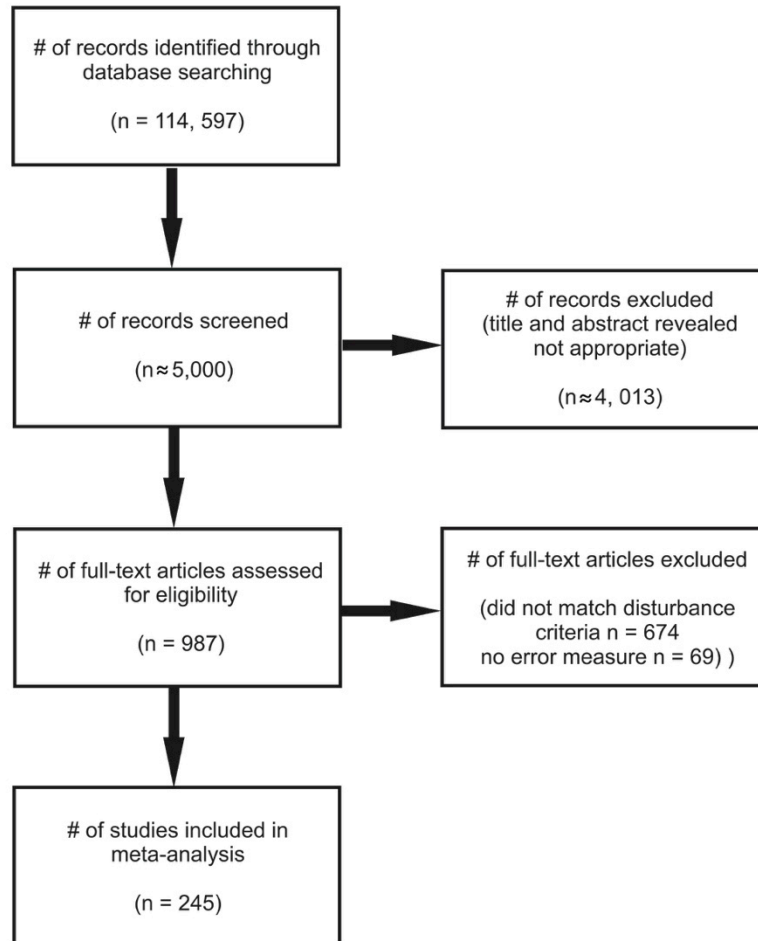
Figure 2.1: Preferred Reporting Items for Systematic reviews and Meta-analyses (PRISMA) diagram. PRISMA flow diagram showing an overview of study selection process.

All papers reported a mean measure of species richness and a corresponding error measure in both a disturbance and a reference condition. Values were given in 147 of the responses. For studies that did not explicitly state results but instead showed results in a figure, as was the case for 180 responses, the average species richness and corresponding error measures were estimated using GetData Graph Digitizer software. If a paper presented multiple responses these were only included when the responses were for different driver categories, different geographical regions, or different trophic categories. Multiple responses that did not differ from each other based on these criteria were averaged, and the average response was used in the dataset. We also averaged responses for studies that manipulated drivers over a range of intensities. Since we had no way of separating the effects of multiple drivers, we only included responses that gave the effects of single drivers. If a combined driver effect was given, the response was not included in the dataset. We took data from the final sampling date for studies that measured species richness over a period of time.

We followed strict guidelines in choosing the types of studies to be included in the analysis. For the temperature increase category we only included studies that increased temperature *per se* (e.g. Chapin et al. 1995). Studies that combined other climate change effects, such as altered light and precipitation, with increases in temperature were not included (e.g. Zhou et al. 2006), nor were observational studies which compared natural communities growing in areas that differ in ambient temperature (e.g. Kennedy 1996). For nutrient addition we included studies that enriched the experimental community with nitrogen (e.g. Bonanomi et al. 2009), phosphorus (e.g. Cherwin et al. 2008), or a fertilizer solution containing one or both of these nutrients (e.g. Lindberg and Persson 2004). Habitat loss and land-use change comprised two separate categories, each with their own sub-categories. We classified a driver as a form of habitat loss if the habitat had been fragmented or reduced in size. If the habitat size remained the same but was transformed from a natural habitat to either an urban or agricultural habitat the driver was classified as land-use change. For habitat loss we included studies that fragmented experimental plots (e.g. Gonzalez and Chaneton 2002), those where habitat size had been reduced (Bonin et al. 2011), or those that compared communities present in control sites to those that had been clear cut or logged (e.g. Biswas and Malik 2010). We did not include

studies that combined corridor effects with fragmentation (e.g. Rantalainen 2004). We grouped three habitat loss categories (fragmentation, reduction in habitat size, and logging) into a single habitat loss category. While the species richness response did differ between the three categories (fragmentation = 13% decline, n = 21; reduction in habitat size = 25% decline, n = 22; logging = 30% decline, n = 15), the difference was not statistically significant, likely due to the high variability within categories caused by low sample sizes (Q_b = 1.96, p=0.38). We decided to group together these three habitat categories to increase the overall sample size for the habitat loss category. All studies in the land-use change category were studies that observed species richness in a site that had been transformed from a natural area to one dominated by human development (e.g.. urban or suburban areas) or agricultural activity, compared to a reference natural area. The species richness response differed between the two land-use change categories (human development = 19% decline, n = 21; agricultural activity = 48% decline, n = 39); however, the difference was not statistically significant (Q_b = 3.05, p=0.081) thus we grouped the two types into a single land-use change category to increase the sample size for this category. Finally, for species invasions we included studies in which a non-native species, or group of non-native species, was added (intentionally or unintentionally) to an established community. We did not include studies that examined the effects of removing non-native species from previously invaded communities (e.g. Ostertag et al. 2009). We also included observational studies that examined an uninvaded site with an invaded site. When invasion studies reported both native and invasive species richness we only included the responses of native species richness.

We grouped studies into one of three species categories. Producers included both terrestrial and aquatic primary producers, ectotherms included animals that rely on external sources to control body temperature, and endotherms included animals that produce heat internally. We chose these three species categories as we wanted to be more specific than simply grouping species as consumers or producers yet separating the studies into anything more specific than these three categories would have resulted in very small sample sizes for each category. Categorizing the consumer species as ectotherms and endotherms takes into account differences in metabolic activity and body size, as endotherms are generally larger bodied animals compared to ectotherms.

The 245 studies spanned most of the Earth's biomes. Ten terrestrial biomes were classified into condensed ecoregions (Bailey 1998): arctic, alpine, northern temperate forest, southern temperate forest, boreal forest, savanna, mediterranean, desert, grassland, and tropical. Freshwater, marine, estuary, and wetland ecosystems were combined into an aquatic biome category. In the categorical analysis of the biomes, effects were only calculated for driver-biome combinations that included five or more responses. Thus, effect sizes were not calculated for 36 of the 55 driver-biome combinations, as they did not fit this minimum sample size. In order to make relevant comparisons across biomes, we only analyzed biomes that contained effect sizes for at least three of the five drivers. This left four biomes in the analysis: northern temperate forest, boreal forest, tropical, and aquatic. The study site latitude was also recorded for each response to examine any potential latitudinal gradients in species loss.

2.3.2 Data Analysis

We performed weighted random effects meta-analyses using MetaWin 2.0 software (Rosenberg and Adams 2000). We considered a random effects analysis, which assumes that effect sizes will exhibit random variation among studies, to be more appropriate than a fixed effects analysis since the studies included in our dataset vary widely in both methodology and biological factors. We used the standard equation for the response ratio (RR) as the effect size for the analyses to compare species richness (SR) between impacted (*i*) and control (*c)* conditions. The response ratio is calculated as:

$$RR = ln\left(\frac{\bar{X}_i}{\bar{X}_c}\right)$$

The response ratio is a common effect size measure in ecological meta-analyses (Hedges et al. 1999). Response ratios that are significantly greater or less than zero indicate a larger change in species richness between the control and treatment, with the direction of change indicating whether the global change driver increased or deceased species richness relative to the reference condition. The percentage of change in the responses that we refer to in the text was calculated as:

$$\% = (e^{RR} - 1) \times 100$$

The independent responses in the analyses were weighted according to their sample variances to account for the difference in statistical precision between individual experiments (Hedges et al. 1999). Greater weight is given to responses whose estimates have a smaller standard error, thus a greater precision. Variance for each response was calculated as:

$$v = \frac{S_i^2}{n_i \bar{X}_i^2} + \frac{S_c^2}{n_c \bar{X}_c^2}$$

We used a combination of categorical and continuous meta-analyses to test for the effect of seven different factors on the magnitude of change in species richness between the control and impacted treatments. The factors were:

1) Driver type (categorical). This factor included five global change driver categories: habitat loss, land-use change, species invasion, nutrient addition, and temperature increase.

2) Study type (categorical). This factor included two study type categories: experimental and observational, but only compared between habitat loss and species invasions, as these were the only two drivers to contain responses from both study types.

3) Species category (categorical): This factor included three species categories: producers, ectotherms, and endotherms.

4) Biome type (categorical): This factor included four biome categories: northern temperate forest, boreal forest, tropical, and aquatic.

5) Initial species richness (continuous): Initial species richness was given as the species richness in the control treatment for each response.

6) Latitude (continuous): Latitude of the study site was given for each response.

7) Experimental length (continuous): Length (in days) was given for each of the experimental responses. Observational studies were not included in this analysis.

We used 95% confidence intervals to determine significant differences in an effect size from zero, indicating an increase or decrease in species richness in the impacted treatment compared to the control. If the confidence interval overlaps with zero then the species richness did not significantly increase or decrease in that response. We also used 95% confidence intervals to compare between the different categories within a factor. If the intervals of two categories overlapped then they are said to not significantly differ in their magnitude of species richness change. In categorical meta-analysis, one can test whether the effect sizes of the categories within a factor are homogeneous, meaning that the observed differences are due to sampling error and not due to the effect of the category by examining the heterogeneity statistic (Q). The total heterogeneity for a group of comparisons (Q_t) is partitioned into within-group heterogeneity (Q_w) and between-group heterogeneity (Q_b). A significant between-group heterogeneity statistic indicates that the effect sizes between the different categories in a factor are significantly heterogeneous and thus the differences are not due to sampling error alone. In the continuous meta-analysis models we used the model heterogeneity (Q_m) to determine if the relationship between the magnitude of species loss and the continuous variable was significant. A significant Q_m indicates that the model explains a significant amount of variability within effect sizes.

2.3.3 Publication Bias

Publication bias occurs when there is a tendency towards publishing only significant results, leading to a disparity in the strength or direction of the results of published studies compared to those of unpublished studies (Moller & Jennions 2001). We used two methods to test for publication bias in our dataset. The first was visual inspection of a 'funnel plot' of sample size against effect size. If the effect sizes were derived from a random sample of studies, suggesting that publication bias is low, the plot should reveal a funnel shape, with small sample sizes showing a larger variance in individual effects and a decrease in variance with increasing sample size (Moller & Jennions 2001). The second method we used to test for publication bias was the calculation of a fail-safe number (Rosenthal 1991). The fail-safe number provides an estimate of the number of future studies needed to change a significant effect to a non-significant one (Moller & Jennions 2001). Therefore, a larger fail-safe number relates to a lower chance of publication bias.

Rosenthal (1991) has suggested that a fail-safe number that is equal to or greater than 5n+10 (where n is the number of studies) provides evidence of a robust effect size that is not skewed by publication bias.

2.4   Results

Our results show that, on average, human-induced environmental changes lead to an 18.3% reduction (n=327) in species richness (Figure 2.2A). Significant decreases in species richness were observed for land-use change (24.8% decline, n=61), species invasions (23.7% decline, n=131), and habitat loss and fragmentation (14% decline, n=60). Significant changes in species richness were not observed for nutrient addition (8.2% decline, n=46) or temperature increase (3.6% decline, n=28). Between-class heterogeneity was marginally insignificant (Q_b = 9.12, p = 0.058), suggesting that the magnitude of species loss slightly differs between the different drivers. When grouped according to experimental or observational study type, which only applied for species invasions and habitat loss, experimental studies had a slightly lower, yet not significantly different, species richness response compared to observational studies (Figure 2.2B). This difference was more pronounced for species invasions, where experimental invasion studies had a lower decline in species richness losing an average of 11.2% less species (n=16) than observational invasion studies, which lost an average of 24.2% of species (n=116). In contrast, species richness response between experimental and observational habitat loss studies was more similar, with experimental studies losing an average of 10.2% of species (n=23) and observational studies losing an average of 17.1% of species (n=37). The between-class heterogeneity was marginally insignificant (Q_b = 6.83, p = 0.078), suggesting that the fraction of decline in species richness slightly differs between the two study type categories.
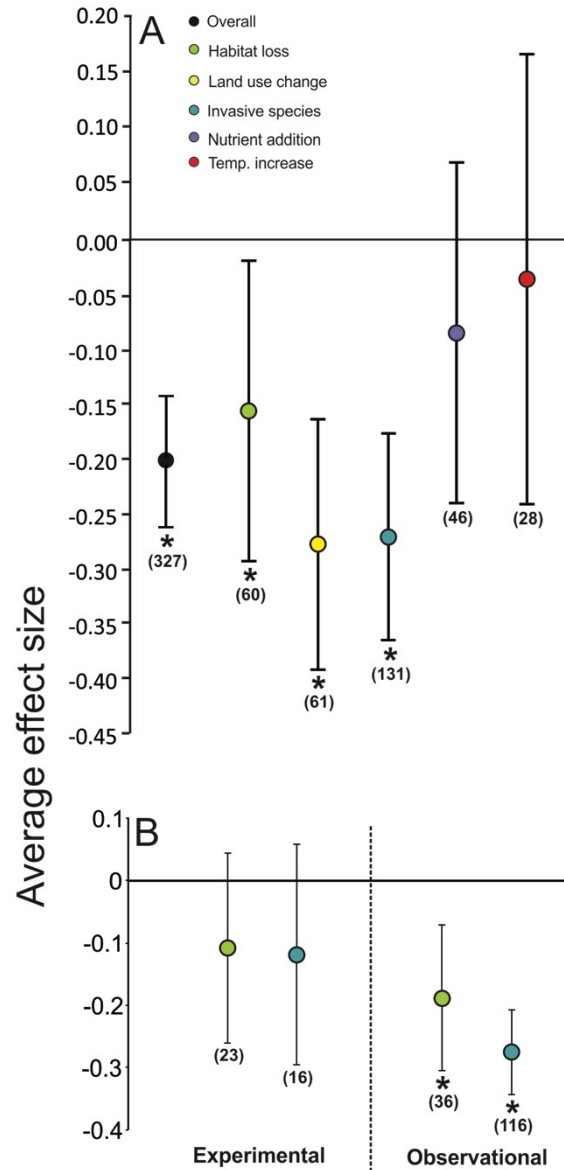
Figure 2.2: Change in species richness following human-induced environmental changes. (**A**) Average response ratios and 95% confidence intervals of species richness across all global change drivers and for each individual driver. (**B**) Average response ratios and 95% confidence intervals of species richness between experimental and observational studies for habitat loss and species invasions across all biomes. The values in parentheses represent the number of responses included in the analysis. Values that significantly differ from zero, according to the 95% confidence intervals, are indicated with an asterisk.

In general, the type of species affected influenced the magnitude of species richness response across all drivers of change (Q_b = 10.59, p = 0.005), and when separated by driver type (Q_b = 25.91, p = 0.011). Across all global change drivers, endotherms showed a greater decline in species richness than ectotherms or producers (Figure 2.3). Endotherms lost an average of 33.2% of species across all drivers while ectotherms lost 10.5%, and producers lost 25.1%. While there was a significant decline in the species richness of endotherms across all drivers, when the drivers were separated none showed a significant decline. The greatest decline in endotherm species was caused by species invasions (44.9%), followed by land-use change (30.5%) and habitat loss (36.7%).

Producer species richness only significantly declined from species invasions (30.3%) and nutrient addition (19.5%). Land-use change (22.2%), habitat loss (13%), and temperature increase (8.9%) all led to insignificant declines in producer species richness. In contrast, land-use change was the only driver to lead to significant decline in species richness in ectotherm species (24%). Habitat loss led to a slightly insignificant decline in ectotherm species (12.8%), while species invasions led to insignificant ectotherm species loss (5.2%), and nutrient addition and increases in temperature led to a small, yet insignificant, increase in ectotherm species richness (15.5% and 5.3%, respectively). Overall, species invasions was the only global change driver to cause significant change in species richness between species categories, resulting in a significantly greater decline in producer species richness (30.3%) compared to ectotherm species richness (5.2%).

Higher initial species richness was associated with greater species loss across all global change drivers (Q_m = 4.61, p = 0.032; Figure 2.4). At low initial richness values, drivers were also generally associated with increases in species richness in impacted habitats. When separated by driver type there was no relation between change in species richness and initial species richness for any of the drivers (Figure A.1).

There was no relationship between latitude and the fraction of change in species richness across all global change drivers or for each driver category (Figure A.2). Experimental length also had no significant effect on the fraction of change in species richness (Q_m = 0.5, p = 0.48; Figure A.3). Heterogeneity statistics and corresponding p-values for all factors included in the meta-analysis are displayed in Table A.1.
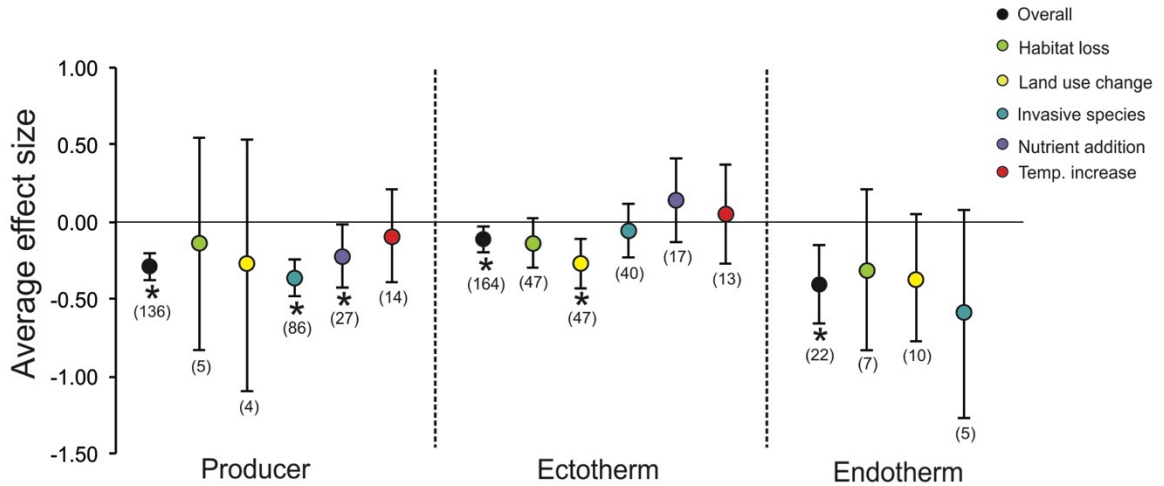
 Figure 2.3: Change in species richness in species categories following human-induced environmental changes. Average response ratios and 95% confidence intervals of species richness changes in producers, ectotherms, and endotherms across all global change drivers and for each driver type. Values that significantly differ from zero, according to the 95% confidence intervals, are indicated with an asterisk. The values in parentheses represent the number of responses included in the analysis.
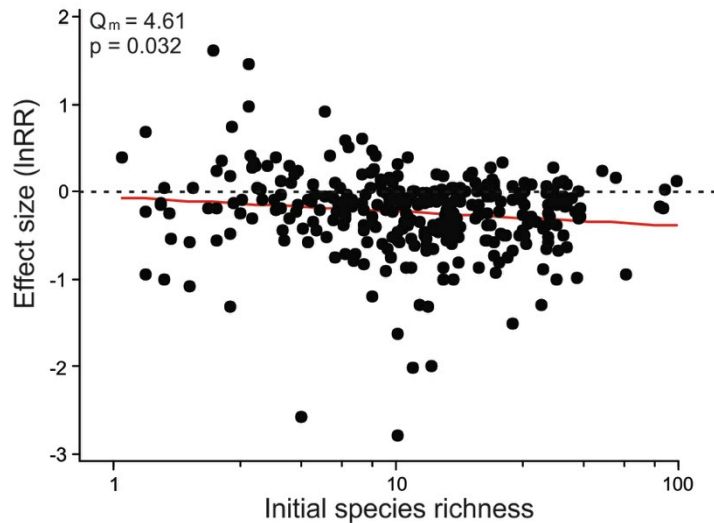
Figure 2.4: Relationship between initial species richness and change in species richness from global change drivers. Species richness in control treatment is used as an indication of initial species richness. Model heterogeneity statistics (Qm) and corresponding p-values are shown.

2.4.1 Drivers Across Biomes

Our results show that the vulnerability of an ecosystem's biodiversity differs across the Earth's biomes. Across all global change drivers, significant decline in species richness was observed in all three of the terrestrial biomes we compared, and no significant change in species richness was observed in the aquatic biome (Figure 2.5). This decline was greatest in the boreal forests with a 25.8% decline in species richness (n=31), followed by the tropics (25.6% decline, n=60), and northern temperate forests (22.5% decline, n=52). Between-class heterogeneity was marginally significant (Q_b = 6.99, p=0.072), suggesting that the decline in species richness slightly differs among the four biome categories across all global change drivers.

None of the five global change drivers led to significant change in species richness in the aquatic biome, and the effect of all drivers did not differ from each other. Comparisons among the drivers of change in the three terrestrial biomes revealed that the drivers led to different magnitudes of change in species richness among the different biomes. Habitat loss led to significant declines in species richness in the tropics (25.6% decline, n=27), yet did not lead to significant declines in either the boreal (17.2% decline, n=17.22) or northern temperate forest (26.7%, n=9) biomes. Land-use change led to the greatest decline in species richness in the tropics (32.4% decline, n=24), yet did not lead to significant decline in the northern temperate forest biome. Species invasions led to the greatest decline in species richness in both the boreal (33.5% decline, n=19) and northern temperate forest (30% decline, n=25) biomes, yet did not lead to significant decline in the tropics (23.7% decline, n=9). Nutrient addition led to insignificant declines in species richness in both the boreal and northern temperate forest biomes.
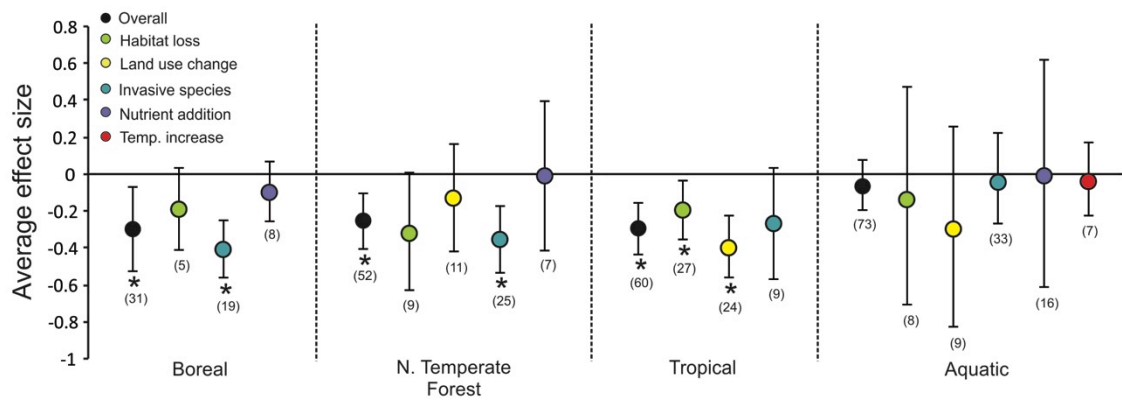
Figure 2.5: Change in species richness across the Earth's biomes following human-induced environmental changes. Response ratios of species richness across all drivers and for each of the five drivers in the boreal forest, northern temperate forest, tropical, and aquatic biomes. Average responses that significantly differ from zero, according to the 95% confidence intervals, are indicated with an asterisk. The values in parentheses represent the number of responses included in the analysis.

2.4.2 Publication Bias

The funnel plot of sample size and effect size displays a clear funnel shape with a much greater spread of studies with small sample sizes and a decrease in this spread as sample size increases (Figure 2.6). This funnel shape is what is expected if the studies are compiled from a random sampling with similar research methods (Moller & Jennions 2001), as it is expected that studies with smaller sample size will be less precise than those with large sample size. The clear funnel shape we see in this plot suggests that our dataset is unlikely to suffer from publication bias. The fail-safe number calculated for our dataset (5548.3) also indicates low publication bias. This number is over three times larger than Rosenthal's (1991) suggested number (5*327+10=1645) thus indicating that the negative effect of human-induced environmental change on species richness is very robust to publication bias.
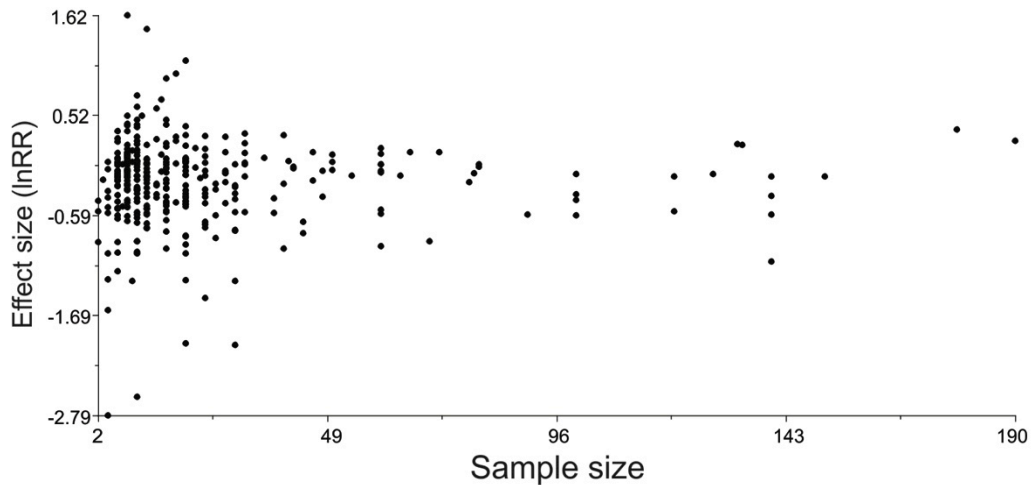
Figure 2.6: Funnel plot used to determine the potential for publication bias. The effect sizes plotted against the corresponding sample sizes for each response in the dataset to identify asymmetry in the distribution of responses. Funnel shape suggests low potential for publication bias.

2.5   Discussion

2.5.1 Change In Species Richness Across Drivers

While habitat loss is widely cited as the leading cause of biodiversity decline (Vitousek et al. 1997; Pimm & Raven 2000; MA 2005) our results show that, at local scales, species invasions result in biodiversity responses that are comparable in magnitude to land-use change and greater than that caused by habitat loss/fragmentation. One potential explanation for this result lies in the difference in the species richness response between observational and experimental studies of species invasions. Observational studies differ from experimental studies in many ways, one being the dispersal ability of species. Dispersal is likely limited in experimental plots while there is more environmental heterogeneity and dispersal potential in observational studies. A greater potential for replacement of lost individuals or species in observational studies implies that the magnitude of species loss might be lower. Our results reveal the opposite pattern, with observational studies of species invasions resulting in a decline in species richness that was over two times greater than the decline observed in experimental invasion studies. This large disparity between study types did not occur for habitat loss. Observational studies of global change are unable to completely control for multiple drivers and it is likely that the impacted treatment will differ in other ways from the reference treatment. Therefore, our results suggest that observational studies of species invasions may be partially confounded by multiple human-induced environmental changes.

Invasive species often establish more frequently in disturbed rather than pristine habitats (Didham et al. 2005), and are often associated with other global change drivers, such as, nutrient addition (Kercher & Zedler 2004) or habitat alteration (MacDougall & Turkington 2005). Thus, the large decline in species richness we observed from species invasions studies may in part be due to synergistic interactions with other global change drivers (Brook et al. 2008). The large, negative effect that we found of land-use change on species richness is not surprising, as previous predictive studies have stressed the impact of land-use change, suggesting that it will be more significant than climate change, nitrogen deposition, and species invasions (Chapin et al. 2000; Sala et al. 2000).

2.5.2 Change In Species Richness Across Taxa

Our analysis of the species richness response between species categories shows that land-use change results in significant declines in species richness in ectotherms, marginally insignificant declines in species richness in endotherms, and insignificant declines in species richness in producers (Figure 2.2). This result supports the hypothesis that global change drivers that transform habitats, including land-use changes, habitat destruction, and habitat fragmentation, are correlated with the extinctions of species in high trophic positions and with large body sizes (Holyoak 2000; Gonzalez et al. 2011).

Species invasions was the only driver that led to significant declines in species richness in producers, and this decline was greater than the decline of ectotherm species following species invasions (Figure 2.3). Endotherm species loss following species invasions was greater than for both producers and ectotherms, yet the sample size was small (n=5), compared to that of the producers (n=86) and ectotherms (n=40), and thus the effect was not significant. These results suggest that species invasions are more likely to lead to local extinctions of producer species than consumer species. A potential explanation of this strong effect of invaders on producer species relates to the nature of the invader species. The studies in our analysis that examined the effect of invasions on ectotherms and endotherms included those where an ectotherm or endotherm species was the invader as well as those where a producer species was the invader. Although not statistically significant, decline in ectotherm species richness was greater in studies where the non-native invader was a producer (5.8% decline, n=27), compared to when an ectotherm species was the invader (0.5% increase, n=13). This pattern was also seen in endotherms, with endotherm species experiencing a 47.8% decline in species richness (n=3) following invasion by a producer species, and a 35% decline in species richness (n=2) following invasion by an endotherm species. These results suggest that non-native species that impact the base of a food web have a stronger effect than higher trophic level invaders. Since all of the studies in our analysis that measured the effect of an invader on producers were those where the non-native invader was also a producer species, the strong effect of producer invaders was likely amplified due to the direct competition the non-native invader had with the native species for resources.

An important caveat to consider when examining changes in species richness

between different studies, is the difference in how finely resolved the taxonomic groups are. There is typically much better characterization among larger animals, such as mammals, compared to small animals, such as invertebrates. Since smaller species may not be as finely resolved, the magnitude of change in species richness in these species may be potentially underestimated. Across all drivers of change, our results show that the decline in endotherm species richness is greater (33.2%) than the decline in ectotherm species richness (10.5%). While this could be due to the hypothesis that extinctions are more highly correlated with large bodied and high trophic level species (Holyoak 2000; Gonzalez et al. 2011), it could also be a result of a difference in how the studies included in our dataset characterized the species.

It is well established that diverse communities are generally more stable in terms of their biomass than communities with lower species richness (Tilman 1999; McCann 2000; Campbell et al. 2011). Our finding that higher initial species richness was associated with greater species loss suggests that the stabilizing role of high diversity on productivity (McCann 2000; Tilman et al. 2006) may not extend to biodiversity maintenance in the face of perturbations. That biodiversity is more difficult to maintain in diverse communities may be related to skewness of species-abundance distributions towards rare species in more diverse communities (Sankaran & McNaughton 1999). There is substantial evidence that rare species are more susceptible to extinction following environmental change than common species (Davies et al. 2004; Lavergne et al. 2005; Gonzalez et al. 2011). Therefore, the high magnitude of decline in species richness we found following habitat loss and species invasions may be, in part, due to the high richness of rare, extinction-prone species in these studies compared to the other disturbances.

2.5.3 Change In Species Richness Across Biomes

We observed a similar magnitude of change in species richness across all global change drivers in the three terrestrial biomes that we compared. However, while all terrestrial biomes experienced an overall significant decline in species richness, the aquatic biome experienced a much lower, and insignificant, decline across all drivers. This suggests that the effect of human-induced environmental changes on species richness is stronger in

24

terrestrial ecosystems. The difference in food web structure and ecosystem properties between aquatic and terrestrial habitats suggests that these systems can differ in their response to global change drivers. The very low effect of species invasions in the aquatic biome (2.4% decline) was surprising given the strong overall effect of invasions across all biomes (23.7% decline) and within each of the terrestrial biomes (boreal = 33.5%, northern temperate forest = 30%, and tropical = 23.7%). A potential explanation for this small effect of species invasions in the aquatic biome is that there may be facilitative interactions occurring between the invaders and native species. There is evidence that non-native species can facilitate native species and potentially lead to increases in native species richness (Simberloff & Von Holle 1999; Rodriguez 2006). The most common mechanism of non-native facilitation of native species is habitat modification, where the invader modifies the natural habitat to create new physical structures, which can benefit native species (Rodriguez 2006). One of the most familiar examples of habitat modification by an invader is the dense, complex colonies formed by invasive bivalves in aquatic ecosystems. These colonies have been shown to cause a shift from planktonic to benthic food webs (Simberloff & Von Holle 1999), and lead to increases in invertebrate diversity (Stewart & Hayne 1994). Of the 33 aquatic species invasion responses in our dataset, we found that the non-native invaders had a positive interaction with the native species in almost half of the responses (19 negative effects vs. 14 positive effects). While facilitative interactions between invaders and native species has been shown to occur almost equally in terrestrial and aquatic habitats (Rodriguez 2006), we did not find the same strong dichotomy in the direction of the effect of species invasions in the terrestrial responses from our dataset (82 negative effects versus 15 positive effects). Therefore, our analysis suggests that positive interactions between invaders and native species may be more common in aquatic ecosystems.

While the magnitude of change in species richness across all drivers was similar among the three terrestrial biomes, we found variation among the biomes in terms of the drivers that had the largest impact on species richness (Figure 2.5). This suggests that the effects of human-induced environmental changes are not uniform across the Earth's biomes. The decline in species richness caused by both land-use change and habitat loss was only significant in the tropical biome. This may be due to the extremely high level of

taxonomic diversity in tropical biomes (Myers et al. 2000), which is particularly affected by a reduction in available living space. On the other hand, species invasions were the only driver to lead to significant decline in species richness in the northern temperate forest and boreal forest biomes. This suggests that species in these biomes are more robust to reduced habitat area, but may be vulnerable to competition for resources imposed by invaders.

Previous attempts to estimate and predict the magnitude of species loss resulting from different global change drivers have relied heavily on expert opinion (e.g. Sala et al. 2000). In contrast, the estimates of declines in species richness presented here are based on empirical studies. In Sala et al. (2000), the authors predict future biodiversity change for five drivers of biodiversity decline (land use, atmospheric CO_2, nitrogen deposition, climate, and biotic exchange) in 11 terrestrial biomes along with lakes and streams. To make these predictions they combine the expected changes in the five drivers with the expected impact of each driver on biodiversity loss. Sala et al. (2000) uses knowledge from experts to estimate the biodiversity impact of each driver in each biome, ranking the estimates from a low impact on biodiversity (1) to a high impact on biodiversity (5). While studies such as Sala et al. (2000) and the present meta-analysis differ in many respects including spatial scale and as such are not directly comparable, a number of the similarities and differences in the results of the two studies are interesting. While land-use change is estimated in Sala et al. (2000) to lead to more species loss across all biomes than any other disturbance, we only find significant declines in species richness resulting from land-use change in the tropics. Species invasions show a much stronger effect on species richness in northern temperate forests and boreal forest biomes based on the meta-analysis presented here than land-use change or habitat loss. Additionally, Sala et al. (2000) predict a relatively low impact of species invasions in these biomes. Our results based on empirical values of change in species richness show that the effect of species invasions on species richness will be much greater than is currently estimated by expert knowledge, and that the effects of species invasions may be comparable to those of land-use change and habitat loss. While it is evident from our analysis that human-induced environmental changes do not all contribute to the same magnitude of change in species

richness in each biome, the large effect of species invasions stresses the significant impact that non-native species have on ecosystems.

An important caveat to consider when comparing our empirical estimates of change in species richness to estimates of global biodiversity change, such as those made by Sala et al. (2000) is how differences in spatial scale can impact the patterns of biodiversity loss. A variety of species richness patterns have been shown to be dependent upon spatial scale. These include differences in the strength or shape of the relationship between diversity and productivity (Chase & Leibold 2002), diversity and latitude (Hillebrand et al. 2004), and diversity and altitude (Rahbek 2004) between local and regional scales. With spatial scale playing a large role in the strength of several species richness relationships, the response of biodiversity to global change drivers may also be scale dependent, and thus the strength of the effects we found may differ at the global scale. It is possible that a driver might decrease local species richness, but increase regional species richness, as could be the case for the effects of nutrient addition if the scale dependent diversity-productivity relationship holds true (Chase & Leibold 2002). A further understanding of the scale-dependence of biodiversity responses to global change drivers will be essential in order to make future biodiversity loss predictions at the global scale.

The latitudinal gradient in species richness from the polar to equatorial regions has been demonstrated for a wide variety of species and is one of the most fundamental patterns of biodiversity (Rosenzweig 1995; Willig et al. 2003). It has been suggested that biodiversity is potentially more difficult to maintain in diverse communities, due to these communities containing many rare species that are more susceptible to extinction following environmental change (Sankaran & McNaughton 1999; Davies et al. 2004). Therefore, we would expect to find a latitudinal gradient in the magnitude of change in species richness following drivers, with low latitude regions that contain greater biodiversity experiencing a greater decline in species richness. However, we did not observe latitudinal gradients in the response of species richness to any of the five drivers of change (Figure A.2). This suggests that while low latitude regions may be more susceptible to species loss due to their high biodiversity, the relative change in local species richness does not differ from higher latitude regions with lower diversity. The issue of spatial scale may also be playing a role in the absence of a latitudinal gradient in our

results. As discussed above, the latitudinal diversity gradient is known to differ between spatial scales, with a stronger and steeper relationship at the regional scale compared to the local scale (Hillebrand et al. 2004). Since our meta-analysis examined change in species richness at the local scale, it is possible that a similar relationship exists, with a weaker relationship between latitude and the magnitude of biodiversity change at the local scale compared to what we might observe at larger scales.

2.5.4 Knowledge Gaps

In compiling the dataset of global change studies for this meta-analysis we found major data gaps, making it impossible to compare the effects of global change drivers across all of Earth's biomes. These gaps are the result of research intensity skewed towards different drivers in different biomes. While human-mediated biodiversity loss has been well studied in some biomes, e.g. boreal and northern temperate forests, information is largely lacking in others. For example, climate change is extensively studied in the arctic and alpine biomes yet few studies have addressed the effects of increases in temperature on biodiversity in northern temperate forest or tropical biomes. Likewise, while species invasions have been well studied in many of Earth's biomes, data is lacking for arctic and alpine biomes. These shortcomings limit our ability to compare the major drivers of biodiversity loss across the Earth's biomes and need to be addressed in order to accurately assess how human-induced environmental changes affect biodiversity at the global scale.

These knowledge gaps seriously hinder our ability to make accurate predictions of future biodiversity change. These shortcomings should be considered when using empirical values of species loss to make predictions of biodiversity change. It will be necessary for future studies to focus on exploring biodiversity change in the areas where knowledge gaps exist to improve projections of future biodiversity change.

2.5.5 Future Directions

In this study we used species richness to measure the magnitude of biodiversity change. Species richness is the most common biodiversity measure used in global change studies, and while it provides a measure of the magnitude of species loss it is unable to account for the complex changes in composition and community structure that can take place

following environmental change (Mendenhall et al. 2012). For example, following deforestation in Costa Rica for agricultural activity bird species richness did not significantly differ between forested and agricultural habitats, suggesting that the deforestation did not have the large negative impact on the community that would be anticipated (Daily et al. 2001). However, community composition differed greatly between habitats, with the natural forest and agricultural area showing two distinct communities (Mendenhall et al. 2011). Changes in the abundance distributions of species in impacted ecosystems are also important indicators of change. Another overlooked problem when using only average values of change in species richness as a metric of biodiversity is that environmental change can also affect the consistency, or predictability, of a response (Fraterrigo & Rusak 2008; Murphy & Romanuk 2012). Response predictability is a relatively unexplored consequence of global change, but an understanding of response predictability changes can help to better interpret the ecological effects of environmental change (Murphy and Romanuk 2012). Future global change studies should concentrate on including alternative measures of biodiversity, such as community composition, along with species richness to obtain a clearer understanding of how different types of human-induced environmental changes affect biodiversity.

2.6   Acknowledgements

CHAPTER 3

DATA GAPS IN LOCAL BIODIVERSITY CHANGE STUDIES ACROSS THE EARTH'S TERRESTRIAL BIOMES

The work presented in Chapter 3 also appears in:

3.1   Abstract

There have been numerous attempts to synthesize the results of local-scale biodiversity change studies, yet several geographic data gaps exist. These data gaps have hindered ecologist's ability to make strong conclusions about how local-scale species richness is changing around the globe. Research on four of the major drivers of global change is unevenly distributed across the Earth's biomes. Here we use a dataset of 638 anthropogenically driven species richness change studies to identify where data gaps exist across the Earth's terrestrial biomes based on land area, future change in drivers, and the impact of drivers on biodiversity, and make recommendations for where future studies should focus their efforts. Across all drivers of change the temperate broadleaf and mixed forests and the tropical moist broadleaf forests are the best studied. The biome-driver combinations we have identified as most critical in terms of where local-scale species richness change studies are lacking include: land-use change studies in tropical and temperate coniferous forests, species invasion and nutrient addition studies in the boreal forest, and warming studies in the boreal forest and tropics. Gaining more information on the local-scale effects of the specific human drivers of change in these biomes will allow for better predictions of how human activity impacts species richness around the globe.

3.2   Introduction

It is well recognized that the Earth's biodiversity is undergoing significant change resulting from various types of human activity (Vitousek et al. 1997; Chapin et al. 2000; Sala et al. 2000; Butchart et al. 2010; Barnosky et al. 2011). Studies that explore changes in species richness resulting from anthropogenic drivers of change are essential to understand how human activity affects biodiversity and have important implications for ecosystem management and policy formation. While a number of attempts to synthesize the data from local-scale biodiversity change studies have been conducted, results have been mixed, with some studies reporting significant decreases in local-scale species richness (Zvereva et al. 2008; Murphy & Romanuk 2014; Gerstner et al. 2014; Newbold et al. 2015) while others have found little to no change (Vellend et al. 2013; Dornelas et al. 2014). Interestingly, the syntheses that have found significant declines in species richness are those that have specifically focused on the effects of human drivers of change, while the syntheses that have found little change in species richness included a variety of locations ranging from disturbed to pristine. The significant changes that have been found in local-scale species richness resulting from human activity highlight the need to further examine where on Earth these changes are occurring and if there are consistent patterns of change in certain biomes resulting from specific drivers. Each of these syntheses have also highlighted similar biases in terms of where local-scale species richness change studies are being conducted, with the majority of studies taking place in North America and Europe. Unfortunately, these data gaps severely limit ecologist's ability to make predictions about where and why local-scale biodiversity change is occurring around the globe.

Several studies have shown that geographic biases exist in the ecological literature (Butchart et al. 2010; Ahrends et al. 2011; Pereira et al. 2010). A 2012 review of terrestrial ecological observations for a five-year period reported an over-representation of studies in temperate biomes and protected areas (Martin et al. 2012). While the overall geographic distribution of ecological studies has been reviewed, geographic biases in local-scale species richness change resulting from anthropogenic drivers have not been analyzed. Given the recent popularity in synthesizing the results of local-scale species richness change studies to make predictions about how local-scale biodiversity is changing

around the globe, a more detailed analysis of the geographical biases that exist in the literature is necessary. In this study, we examine the geographic biases that exist in terrestrial local-scale species richness change studies and provide information about where future local-scale species richness change studies need to be conducted. We specifically focus on species richness change resulting from anthropogenic global change drivers (land-use change, species invasions, nutrient addition, and warming). We examine how the geographic biases differ for these drivers across the Earth's terrestrial biomes and determine the data gaps that exist based on three circumstances: (1) the land area that the biome covers, (2) the future change that the drivers are projected to have in each biome, and (3) the impact that the drivers have on biodiversity of each biome.

The sensitivity of a particular biome to a global change driver will depend on the unique set of features that define the biome, and thus it is expected that the effects of various global change drivers will differ across the Earth's biomes (Sala et al. 2000). For example, the impacts of climate change on productivity have been shown to differ widely among the Earth's biomes (Zhang et al. 2013; Silva & Anand 2013). Various studies have assessed the magnitude of global change drivers across the Earth's biomes and have provided estimates of which biomes are most vulnerable to certain drivers. The projections of future change across biomes resulting from various global change drivers demonstrates that certain data gaps in local-scale species richness change studies might be justified based on the level of threat of a particular driver in a specific biome. For example, estimates of land-use change for the year 2050 predict large proportions of future land-cover change in temperate broadleaf and mixed forests along with temperate and tropical coniferous forests, and project a much lower proportion of change in the tundra and boreal forest biomes (Lee & Jetz 2008). Therefore, we would expect to find the majority of studies examining the effects of land-use change on local-scale species richness to have been conducted in temperate forests and tropical coniferous forests. Projections of net change in the number of 100 of the world's worst invasive alien species for the year 2100 (Bellard et al. 2013) estimates that the highest increase of invasive species will occur in temperate mixed forests. Therefore, an over-representation of invasion studies in the temperate forest biomes is well justified. By comparing the data gaps in local-scale species richness change studies with estimates of which biomes will be

most and least affected by global change drivers we aim to identify the most critical data gaps and make suggestions as to where future local-scale species richness change studies need to be conducted to fill in these gaps.

Knowledge of how global change drivers will impact local-scale species richness and how these impacts compare across biomes is dependent upon available information of these impacts across the Earth's biomes, for which the ecological literature is currently lacking. The findings from large-scale syntheses of local-scale species richness change will play crucial roles in how human-impacted ecosystems are managed in the future. Unfortunately, predictions for how human activity will impact local-scale biodiversity around the globe are seriously hindered by the data gaps that exist in the literature. It is necessary for future biodiversity research to focus on biodiversity change in biomes that are expected to experience significant impacts from a human driver of change and where data on that driver is lacking. Here we use a dataset of 767 responses of change in species richness taken from 638 human-mediated species richness change studies to determine where geographic data gaps exist across the various global change drivers, and discuss whether these biases are justified based on the varying levels of threat that the drivers pose to the biomes.

3.3   Methods

3.3.1   Selection Criteria

Our dataset was compiled by searching the biological literature for studies that reported the effects of anthropogenic drivers of change on local-scale species richness in a terrestrial habitat. Four anthropogenic drivers of change that have been identified as major drivers of current biodiversity change were included in the dataset: land-use change, species invasions, nutrient addition, and warming (Vitousek et al. 1997). We performed a literature search using the ISI Web of Science database using the following search expressions: "biodiversity " OR "species richness" OR "community change" AND ("invasi* species" OR "habitat loss" OR "land use change" OR "climate change" OR "warm*" OR increas* temperature" OR "eutrophication" OR "nutrient add*").   We also searched for studies in the references of relevant meta-analyses and syntheses. A final

search of the literature was completed on 17 October 2015. We included studies that experimentally manipulated one of the four drivers of change or observational studies that compared an impacted site with a control (non-impacted) site. The literature search yielded 638 suitable studies with 767 values of change in species richness that were included in the final dataset. Only studies conducted in terrestrial ecosystems were included in the dataset. This dataset specifically focuses on studies that examine change in species richness in control vs. impacted treatments. Studies that assessed other metrics like evenness and biodiversity indices, those that assessed changes in community composition, and those that examined species richness change using time-series or before-after studies were not included in the dataset. We chose to focus only on species richness, as it is the most common biodiversity measure used in studies examining the impact of anthropogenic global change drivers.

Geographic coordinates were either taken from the papers or in cases where the coordinates were not given they were estimated using Google Earth (Google Inc). Studies that reported multiple measures of species richness for the same geographic location (i.e. different species, driver intensities, etc.) were only included in the dataset once and the values were averaged when calculating effect sizes. We only included multiple responses from the same study when they were taken from different countries or biomes. The selection criterion is similar to that in Murphy & Romanuk (2014) and a more detailed explanation can be found there. For the purposes of examining data gaps, the habitat loss and land-use change categories have been combined. Also, for the current study we only included invasion studies that give a measure of species richness change in the entire community rather than just native species.

3.3.2 Data Analysis

To investigate the data gaps existing across the Earth's biomes we categorized study responses using the 14 global terrestrial ecoregions identified by Olson et al. (2001). We visualized the global distribution of studies by entering the locations of all 767 responses into ArcGIS 10.1 (ESRI 2011). We used chi-squared tests to determine if specific biome-driver combinations are over-represented or under-represented. We tested for significant differences between the observed and expected distribution of studies based on three sets

of circumstances: (1) the relative land-area that the biome covers (e.g. biomes with a larger land area are expected to contain a proportionately greater number of responses), (2) the future change that the drivers are projected to have in each biome (e.g. biomes projected to experience a larger increase in a driver are expected to contain a greater number of responses), and (3) the impact that the drivers have on biodiversity in each biome (e.g. biomes where a driver has a larger impact on biodiversity are expected to contain a greater number of responses). We used projections from various studies to determine the future change of drivers among biomes. For land-use change we used the projected proportions of land-cover transformation due to land-use change for the year 2050 given in Lee & Jetz (2008). Estimates are given for 57 biome-realm combinations and for four socio-economic scenarios. We averaged the estimates for the biome-realm combinations and across the four socio-economic scenarios to get one estimate of future land-use change for each biome. Using these estimates we determined the proportion of projected land-use change for each biome for the year 2050 (Table 3.1). For species invasions we used estimates of the percentage of net change in the numbers of 100 of the world's worst invasive species for the year 2080 given in Bellard et al. (2013). The biomes categorized in this study slightly differ from our categorization so in some cases the estimates from multiple biomes were averaged. Since this study estimates that some biomes will become less suitable for invasive species (i.e. the tropics), the values given for percentage of net change are negative. To calculate the proportion of change in invasive species for each biome and the expected number of studies we first added 5 to each estimate, thus making all estimates positive (Table 3.1). For nutrient addition we used the expected changes for the year 2100 given in Sala et al. (2000). This study ranks the biomes from 1-5 based on future change in nitrogen deposition, and using these ranks we calculated the proportion of change for each biome (Table 3.1). To determine the expected number of warming studies based on future change we used the climate anomalies between pre-industrial conditions and projections for the year 2100 given in Benito-Garzon et al. (2014) (Table 3.1). To calculate the expected number of studies based on the impact that the drivers have on the biodiversity of each biome we used the estimates given in Sala et al. (2000) where the impact of a large change in each driver on

biodiversity are ranked from 1-5 for each biome. The proportion of impact that each driver has on each biomes biodiversity was calculated from these rankings (Table 3.1).

We conducted a separate chi-squared test for each driver of change and used the total number of studies for each driver to calculate the expected number of studies. For example, the total number of land-use change studies across all biomes is 342, therefore, to calculate the expected number of studies in each biome for the chi-squared test based on land area we multiplied the proportion of land area that each biome covers by 342 to give the expected values. These values were then compared to the observed number of studies in each biome in the chi-squared test. Biome-driver combinations were considered significantly over or under-represented if the p-value was equal to or less than 0.05.

We used the standard deviation of the average effect sizes for each biome-driver combination as a measure of how variable the magnitude of change in species richness is in each biome. The effect size compares species richness between the control (c) and impacted (i) treatments in each study and was calculated as the response ratio (Hedges et al. 1999): $RR = ln\left(\frac{\bar{x}_i}{\bar{x}_c}\right)$.

3.4   Results

3.4.1 Global Study Distribution

Our results reveal several biases in the global distribution of anthropogenically driven, local-scale species richness change studies. Studies included in the dataset were conducted in 79 countries. The five countries with the greatest number of responses were: USA (23.6% of responses), China (8.1% of responses), Brazil (6.5% of responses), Canada (5% of responses), and Australia (3.7% of responses). The Palearctic and Nearctic are the most commonly studied biogeographic realms with 33.8% and 28.6% of studies conducted in these realms, respectively. Across all studies, the Afrotropic and Antarctic realms are significantly under-represented based on land area (p < 0.001 and p = 0.021, df = 7, respectively), while the Nearctic and Oceanic realms are significantly over-represented (p < 0.001, df = 7). Based on land area, land-use change studies are significantly over-represented in the Neotropics (p < 0.001, df = 7) and are significantly under-represented

in the Palearctic (p = 0.001, df = 7). Both species invasion and nutrient addition studies are significantly under-represented in the Afrotropics (p = 0.014 and p < 0.001, df = 7, respectively) and significantly over-represented in the Nearctic and Oceanic (p < 0.001, df = 7) realms. Warming studies are significantly over-represented in the Nearctic realm (p < 0.001, df = 7).

3.4.2 Study Distribution By Biome

Across all drivers, temperate broadleaf and mixed forests (31%) and tropical moist broadleaf forests (23%) are the most frequently studied biomes (Figures 3.1 and 3.2). All other biomes contain fewer than 10% of responses. Based on land area, the boreal forest and tropical grassland biomes are significantly understudied (p < 0.001, df = 12), while the temperate broadleaf and mixed forest, temperate coniferous forest, tropical moist broadleaf forest, and Mediterranean biomes are significantly over-represented (p < 0.001, df = 12).
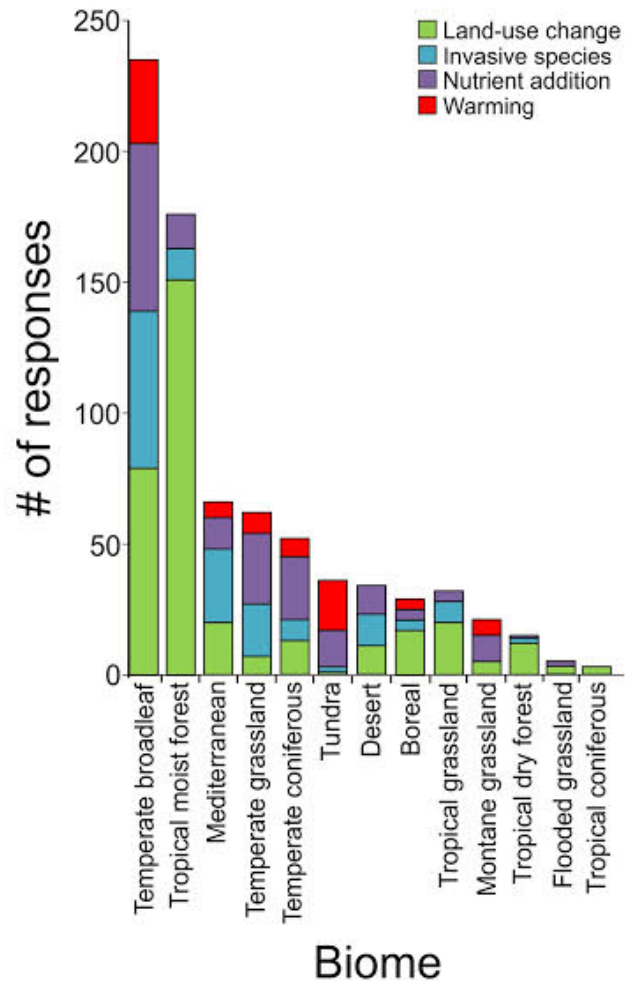
Figure 3.1: Number of local-scale species richness change study responses across 13 terrestrial biomes and four human drivers of change.

There is notable disparity in how frequently studied a biome is when the four drivers of change are examined separately (Figures 3.1 and 3.2). One of the most significant areas of bias in our analysis of human driven local-scale species richness change studies is the over-representation of land-use change studies in tropical and temperate broadleaf forest biomes. Almost half of the land-use change studies are conducted in tropical moist broadleaf forests and almost a quarter of land-use change studies are conducted in temperate broadleaf and mixed forests. Based on the proportion of land area that these biomes cover they are significantly over-represented, with three times the number of expected land-use change responses in the tropical moist broadleaf forest ($p < 0.001$, df = 12), and over two times the number of expected responses in the temperate broadleaf and mixed forest ($p < 0.001$, df = 12). All other biomes contain less than 6% of the land-use change studies (Figure 3.1), and based on land area the tundra and desert biomes are under-represented ($p = 0.007$ and $p < 0.001$, df = 12, respectively). When analyzed based on the projection of future land-use change and the impact that land-use change has on the biodiversity of each biome the tropical moist broadleaf forest remains over-represented in both categories ($p < 0.001$, df = 12). The temperate broadleaf and mixed forest biome is over-represented based on the impact on biodiversity ($p < 0.001$, df = 12), but not based on projected future land-use change. Both the temperate and tropical coniferous forest biomes are significantly under-represented based on the magnitude of land-use change expected to occur in these biomes in the future ($p < 0.001$, df = 12), and the tropical coniferous forest is almost significantly under-represented based on the impact to biodiversity ($p = 0.055$, df = 12). The temperate grassland and tropical dry forest biomes have the lowest variance in the magnitude of species richness change following land-use change (SD = 0.149, n = 7 and SD = 0.2, n = 12, respectively), while the desert and tropical coniferous forest biomes have the highest variance (SD = 0.793, n = 11 and SD = 0.869, n = 3, respectively) (Figure B.1).

Studies that examine the effect of species invasions on local-scale species richness change are significantly over-represented in the temperate broadleaf and mixed forests ($p < 0.001$, df = 12; 38% of studies) based on all three categories (Table 3.1). Species invasion studies are also over-represented in the Mediterranean biome based on land area ($p < 0.001$, df = 12; 18%), but not based on the projected extent of exotic invasions and

the impact of invaders on Mediterranean biodiversity. Invasion studies are relatively well represented in temperate grasslands, deserts, and tropical moist broadleaf forests, yet all other terrestrial biomes contain 5% or fewer of the invasive species responses (Table 3.1). The tundra and boreal forest biomes have the lowest variance in the magnitude of species richness change following species invasions (SD = 0.021, n = 2 and SD = 0.085, n = 4, respectively), while the temperate broadleaf forest (SD = 0.558, n = 60), temperate grassland (SD = 0.606, n = 20), and Mediterranean (SD = 0.559, n = 28) biomes have the highest variance (Figure B.1).

Over half of nutrient addition studies are conducted in the temperate region (Figure 3.1; Table 3.1). Based on land area, nutrient addition studies are significantly over-represented in temperate broadleaf and temperate coniferous forests (p < 0.001, df = 12), but temperate broadleaf and mixed forests are the only biome that is significantly over-represented based on the projected levels of future nutrient addition and the impact on biodiversity (Table 3.1). Nutrient addition studies are well represented in the tundra, yet fewer are conducted in the boreal forest (Table 3.1). The flooded grassland (SD = 0.046, n = 2), temperate grassland (SD = 0.151, n = 27), and tundra (SD = 0.159, n = 14) biomes have the lowest variance in the magnitude of species richness change following nutrient addition, while the tropical moist forest (SD = 0.928, n = 13) and boreal forest (SD = 0.474, n = 4) biomes have the highest variance (Figure 3.1).

Similar to the other drivers, warming studies are over-represented in temperate broadleaf and mixed forests based on land area, projections of future change, and impact on biodiversity (p < 0.001, df = 12; 39% of studies). Warming studies are also well represented in the tundra biome (23%), yet are lacking in the boreal forest (5%) and non-existent in the tropics with zero warming studies conducted in tropical grasslands and the three tropical forest biomes (Figure 3.1, Table 3.1). The temperate grassland (SD = 0.142, n = 8), and temperate broadleaf forest (SD = 0.17, n = 32) biomes have the lowest variance in the magnitude of species richness change following warming, while the montane grassland (SD = 0.53, n = 6) and tundra (SD = 0.564, n = 19) biomes have the highest variance (Figure B.1).
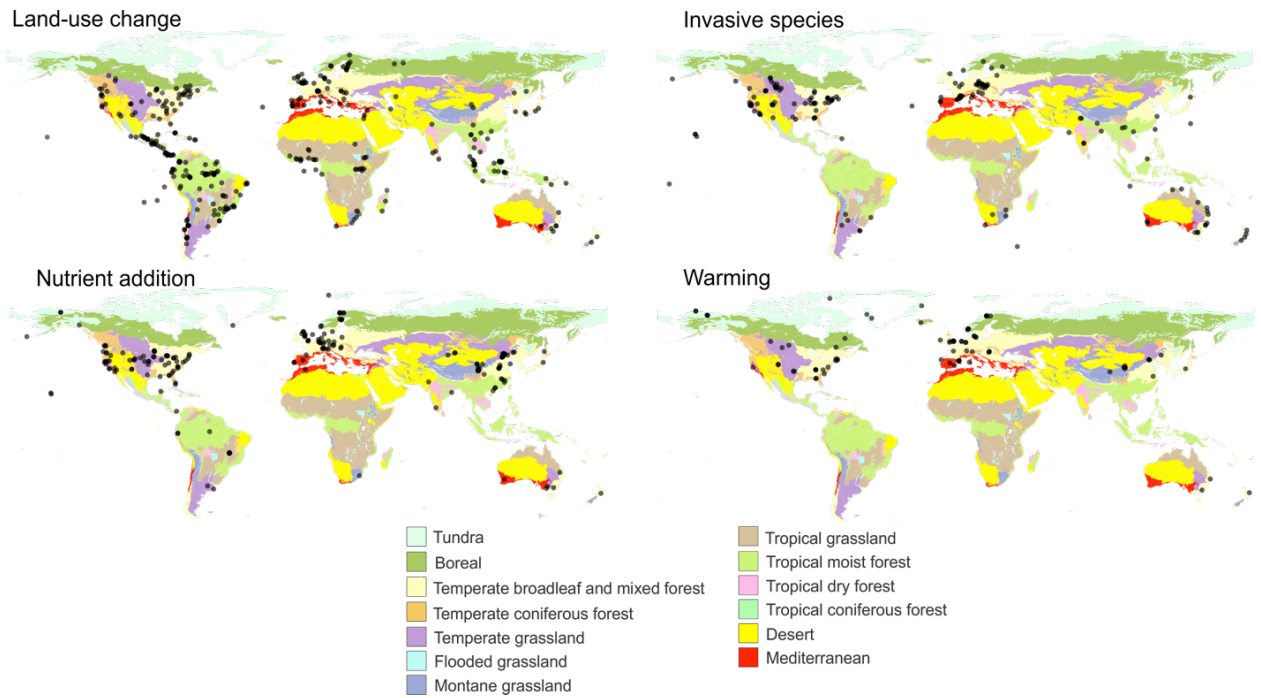
Figure 3.2: Global distribution of local-scale species richness change studies for four human drivers of change. Points are semitransparent with darker areas indicating an overlap of studies.

Table 3.1: Actual and expected percentages of human-induced local-scale species richness change studies conducted in each biome for four drivers of change. along with the expected percentage of studies based on: 1) the land area covered by each biome, 2) the project future change, and 3) the impact of the driver on biodiversity. Values highlighted indicated that the biome-driver combination is significantly over- (blue) or under- (red) represented (p < 0.05) based on the highlighted circumstance.

	Biome	% of actual studies	Percentage of expected studies based on:		
			Land area	Projected future change	Impact on biodiversity
Land-use change	Tundra	0.29	8.6	0.1	7.7
	Boreal	4.97	11.2	0.8	7.7
	Temperate broadleaf forests	23.1	9.5	14.2	7.7
	Temperate coniferous forests	3.8	3	17	7.7
	Temperate grasslands	2.05	7.5	0.8	7.7
	Flooded grasslands	0.88	0.8	8.7	7.7
	Montane grasslands	1.46	3.8	6	7.7
	Tropical grasslands	5.85	15	10	7.7
	Tropical moist broadleaf forests	44.15	14.7	8	7.7
	Tropical dry broadleaf forests	3.51	2.2	9	7.7
	Tropical coniferous forests	0.88	0.5	20	7.7
	Deserst and xeric shrublands	3.22	20.7	3	7.7
	Mediterranean	5.85	2.4	1.8	7.7
Species invasion	Tundra	1.27	8.6	9.88	4.2
	Boreal	2.55	11.2	11	4.2
	Temperate broadleaf forests	38.21	9.5	13.89	9.4
	Temperate coniferous forests	5.1	3	12.81	9.4
	Temperate grasslands	12.74	7.5	7.85	8.3
	Flooded grasslands	0	0.8	1.90	8.3
	Montane grasslands	0.63	3.8	5.85	8.3
	Tropical grasslands	5.1	15	4.45	8.3
	Tropical moist broadleaf forests	7.64	14.7	4.98	6.3
	Tropical dry broadleaf forests	1.27	2.2	4.47	6.3
	Tropical coniferous forests	0	0.5	1.14	6.3
	Deserst and xeric shrublands	7.64	20.7	12.41	8.3
	Mediterranean	17.83	2.4	12.41	12.5
Nutrient addition	Tundra	7.53	8.6	5.9	11.5
	Boreal	2.15	11.2	8.8	11.5
	Temperate broadleaf forests	34.41	9.5	8.8	11.5
	Temperate coniferous forests	12.9	3	8.8	11.5
	Temperate grasslands	14.52	7.5	8.8	7.7
	Flooded grasslands	1.08	0.8	8.8	7.7
	Montane grasslands	5.37	3.8	8.8	7.7
	Tropical grasslands	2.15	15	8.8	7.7
	Tropical moist broadleaf forests	6.98	14.7	5.9	3.8
	Tropical dry broadleaf forests	0.53	2.2	5.9	3.8
	Tropical coniferous forests	0	0.5	5.9	3.8
	Deserst and xeric shrublands	5.91	20.7	5.9	3.8
	Mediterranean	6.45	2.4	8.8	7.7
Warming	Tundra	23.17	8.6	10.39	10.1
	Boreal	4.87	11.2	9.38	8.9
	Temperate broadleaf forests	39.02	9.5	7.42	5.1
	Temperate coniferous forests	8.53	3	7.56	5.1
	Temperate grasslands	9.76	7.5	7.38	7.6
	Flooded grasslands	0	0.8	7.82	7.6
	Montane grasslands	7.32	3.8	6.75	7.6
	Tropical grasslands	0	15	7.85	7.6
	Tropical moist broadleaf forests	0	14.7	8.06	7.6
	Tropical dry broadleaf forests	0	2.2	7.44	7.6
	Tropical coniferous forests	0	0.5	6.36	7.6
	Deserst and xeric shrublands	0	20.7	7.63	10.1
	Mediterranean	7.32	2.4	5.96	7.6

3.5   Discussion

It is evident that research intensity in the various terrestrial biomes is skewed towards
different anthropogenic drivers of change. Below we discuss the differences in research
intensity across biomes for each of the four human drivers of change, and identify the
most critical data gaps in terms of where future human driven local-scale species richness
change studies need to be conducted.

3.5.1 Land-Use Change

The majority of land-use change studies are conducted in tropical moist forests and
temperate broadleaf forests. It is not surprising that land-use change studies are most
common in these biomes as habitat loss due to human activity and land conversion has
been most extensive in tropical and temperate forests (Miles et al. 2006; Potapov et al.
2009). Estimates of land-use change for the year 2050 project an 11.5% change in land-
cover in tropical moist forests and a 19.5% change in tropical broadleaf and mixed forests
worldwide (Lee & Jetz 2008). While the projections of future land-cover change in these
two biomes are large, there are other biomes with higher proportions of projected land-
cover change that are much less studied. These include temperate coniferous and tropical
coniferous forests, which are projected to experience 23% and 28% land-cover change,
respectively, by the year 2050 (Lee & Jetz 2008), yet very few land-use change studies that
examine changes in local-scale species richness are conducted in these biomes. This lack
of studies is particularly concerning for tropical coniferous forests as not only is this biome
significantly under-represented based on both projections for future change and the
impact of change on biodiversity but tropical coniferous forests also have the highest
variance in the magnitude of local-scale species richness change following land-use
change of all the biomes (Figure B.1). Compared to the other biomes, the variance in the
magnitude of local-scale species richness change following land-use change is also
relatively high in the tropical moist forests so the large number of land-use change studies
conducted in this biome is justified (Figure B.1). However, given the significant impact
that land-use change has on biodiversity (Newbold et al. 2015), shifting some of the focus
of future land-use change studies from tropical moist and temperate broadleaf forests to

the coniferous forest biomes would fill crucial data gaps in how land-use change impacts biodiversity around the globe.

3.5.2 Invasive Species

Studies that examine the effect of species invasions on local-scale species richness are most commonly conducted in temperate broadleaf forests (38% of responses) and the Mediterranean (18% of responses). Invasions by exotic species are most likely in regions of high human activity (Didham et al. 2005; MacDougall & Turkington 2005) such as the Mediterranean, temperate forest, and grassland biomes, as opposed to remote areas, such as the tundra and boreal forest (Sala et al. 2000). The over-representation of invasion studies in the temperate broadleaf and mixed forest biome is well justified as it has been estimated that temperate mixed forests will experience a high increase of invasive alien species for the year 2100 (Bellard et al. 2013). Our results also show that the temperate broadleaf forest and Mediterranean biomes have high variance in the magnitude of change in local species richness following species invasions so while these biomes are significantly over-represented further studies in these biomes will be useful in deciphering this variability (Figure B.1).

We found relatively few species invasion studies conducted in the tropical biomes (8% in tropical moist forests, 5% in tropical grasslands, 1% in tropical dry forests, and none in tropical coniferous forests) compared to the large number of total studies conducted in this biome. Species invasions are not thought to be one of the major threats to biodiversity in the tropical biomes as the high diversity in the tropics minimizes the chance of non-native species successfully invading (Sala et al. 2000). Also, as temperatures increase fewer species will be able to successfully inhabit the tropics. Bellard et al. (2013) predicts that the shift of tropical forests to more extreme climates compared to higher latitude biomes will lead to the tropics becoming less suitable for invasive species in the future. Therefore, the distribution of invasion studies throughout the tropical biomes is appropriate to the level of threat that invasions will have in these areas in the future.

Less than 3% of the invasion studies in our dataset are conducted in the tundra and boreal forest biomes. These biomes also have the lowest variation in the magnitude of change in local species richness following invasions compared to the other biomes.

Therefore, the few studies conducted in the tundra and boreal forest all show very similar change in species richness from species invasions suggesting that the low number of studies in these biomes is justified. However, increasing temperatures are resulting in dramatic northward species range shifts (Chen et al. 2011) and warmer temperatures and longer growing seasons are enabling the survival of more non-native species to high-latitude ecosystems (Carlson & Shephard 2007; Spellman et al. 2014). The ecological effects of the increasing number of exotic species inhabiting the boreal forest are poorly understood (Sanderson et al. 2012). The boreal forest plays a key role in various processes that are crucial for global ecosystem functioning, such as biogeochemical cycling (Volney & Fleming 2000), and given the detrimental effects of invasive species on native biodiversity and ecosystem functioning (Vitousek et al. 1996; Murphy & Romanuk 2014), additional studies of the effects of species invasions on boreal forest biodiversity would be useful.

3.5.3 Nutrient Addition

The addition of excess nutrients to ecosystems is expected to be most prevalent in regions of high industrialization and intense agricultural activity (Galloway et al. 2004). Studies that examine the effects of nutrient addition on local-scale species richness are most common in temperate broadleaf and mixed forests (34% of responses). Furthermore, while studies of the three other human drivers of change are lacking in the temperate coniferous forest there are a relatively high number of nutrient addition studies conducted in this biome (13% of responses). The temperate regions of the Earth have large population density and increasing agricultural activity (Sala et al. 2000). Nutrient addition is expected to be a major driver of future biodiversity change in the temperate forest biomes; therefore the over-representation of studies in the temperate forests is not surprising. The variance in the magnitude of change in local species richness following nutrient addition is also relatively high in both temperate forest biomes, which further justifies the over-representation. Nutrient addition studies are disproportionately conducted in temperate forest and tundra biomes and understudied in the boreal forest biome (2% of responses). Nutrient addition is not expected to have as large an impact on biodiversity in the tropical forest and desert biomes since plant growth in these regions is

primarily limited by water availability rather than nitrogen (Vitousek 1984), yet we found more nutrient addition studies conducted in these biomes (7% and 6% of responses, respectively) than in the boreal forest. Like the tundra biome, nutrient addition in the boreal forest is not generally acknowledged as an immediate threat due to its distance from sources of pollution (Sala et al. 2000). However, atmospheric nitrogen deposition from agricultural and industrial activity is currently increasing and has the potential to be transported long-ranges, resulting in impacts on remote ecosystems (Bergstrom et al. 2006; Holtgrieve et al. 2011). The boreal forest is an example of a relatively pristine ecosystem that could suffer immense consequences from increased atmospheric nitrogen deposition, as boreal forest plant species are nitrogen-limited. Furthermore, the high variance in the magnitude of change in species richness following nutrient addition in the boreal forest suggests that more studies are necessary to determine how boreal forest biodiversity responds to nutrient addition.

3.5.4 Warming

Warming studies are most common in temperate broadleaf and mixed forests (39% of responses) and are better represented in the tundra biome compared to the other four drivers of change (23% of responses). Global circulation models predict larger increases in temperature at higher latitudes (Kattenberg et al. 1996), thus is it not surprising that the majority of studies examining the effects of increasing temperatures on species richness are conducted in these high latitude biomes. Interestingly, the magnitude of change in species richness is highly variable in the tundra biome and is much less variable in the temperate broadleaf and mixed forests (Figure B.1). This suggests that future studies should focus more on the impacts of warming on tundra biodiversity than on temperate broadleaf forest biodiversity, which is the opposite to what is currently occurring.

Only 5% of warming studies are conducted in the boreal forest yet, given its high latitude, this biome is expected to experience significant increases in temperature compared to other biomes. None of the warming studies included in our dataset are conducted in tropical grassland, tropical forests, and desert biomes. While these lower latitude biomes are not expected to experience as large an increase in temperature compared to higher latitude biomes, such as the boreal forest and tundra (Sala et al.

2000), the ecological communities present in these biomes are expected to be less robust than species at higher latitudes to the effects of warming (Sunday et al. 2011). It has been suggested that the lower thermal tolerance of tropical species will result in increasing temperatures to have more detrimental effects on tropical communities (Tewksbury et al. 2008; Tuck & Romanuk 2012). The difference in the effects of climate change along latitudinal gradients highlights the need to conduct studies and collect data on the effects of warming on species richness across all of the Earth's biomes, not just those where temperatures are expected to increase the most.

3.5.5 Conclusions

In this study we identify terrestrial biomes where studies that examine the effects of certain human drivers on local species richness are severely lacking based on the level of threat that the drivers pose to the biomes. The biome-driver combinations that are most critical in terms of where future biodiversity change studies need to be conducted are: land-use change studies in temperate and tropical coniferous forests, species invasion and nutrient addition studies in the boreal forest, and warming studies in the boreal forest and tropical biomes.

An important caveat to our identification of data gaps is that we only consider studies that examine the effects of human drivers on species richness in control vs. disturbed treatments. There are a variety of other biodiversity change studies that were not included in this analysis. We chose to focus only on species richness, as it is the most common biodiversity measure used in studies examining the effects of human drivers of ecosystem change. However, we expect roughly similar data gaps and patterns across biomes for studies that use biodiversity metrics other than species richness.

3.6   Acknowledgements

CHAPTER 4

PREDICTABILITY OF COMMUNITY RESPONSES TO HUMAN-INDUCED
ENVIRONMENTAL CHANGES

The work presented in Chapter 4 also appears in:

4.1   Abstract

Disturbances often lead to changes in average values of community properties; however, disturbances can also affect the predictability of a community's response. We performed a meta-analysis to determine how response predictability, defined as among-replicate variance in diversity and community abundance, is affected by species loss and four human-induced environmental changes that are major drivers of global change (species invasions, nutrient addition, temperature increase, and habitat loss). We further determined whether response predictability differed according to habitat and trophic role. Species removals and nutrient addition decreased response predictability, while species invasions increased response predictability. In aquatic habitats, global change drivers generally led to a decrease in response predictability, whereas terrestrial habitats showed no overall change in response predictability, suggesting that differences in food web and ecosystem structure affect how communities respond to drivers of global change. Producers were also more likely to show decreases in response predictability, particularly following species removals, highlighting widespread destabilizing effects of species loss at the producer level. Overall, our results show that, whether or not global change drivers lead to changes in response predictability is highly contingent on driver type, habitat, and trophic role. The nature of changes in response predictability will likely play a major role in how communities recover from environmental change.

4.2   Introduction

The structural properties of communities subjected to disturbances often differ from those of undisturbed communities. This includes differences in diversity and abundance, as well as in the dynamic nature of population and community fluctuations (Syms & Jones 2000; Keitt 2008). The changes that occur following disturbances can have major impacts on community functioning (Ives & Carpenter 2007). Most studies that have examined how disturbance affects community structure have focused on how average values of community properties, such as diversity or abundance, change with disturbance. However, disturbance can also affect the consistency, or predictability, of a response (Fraterrigo & Rusak 2008). Response predictability, which measures the extent of divergence in community structure, is defined as the variation among-replicates of the same experimental treatment (McGrady Steed et al. 1997; Carpenter & Brock 2006), and is most often represented as the standard error (Forrest & Arnott 2007).

The recent emphasis in ecology on the relationship between biodiversity and ecosystem functioning has highlighted the importance of determining how environmental change affects stability or predictability in structure and function over time (Loreau et al. 2000; Cottingham et al. 2001; Cardinale et al. 2006; Jiang & Pu 2009; Campbell et al. 2011). Disturbances also affect the predictability of communities in space, such that structural and functional features of disturbed communities can become more or less predictable relative to communities that have not been subjected to disturbance (Naeem & Li 1997; Morin & McGrady-Steed 2004).

Change in variability among replicates is a relatively unexplored consequence of disturbance but is an important outcome, both ecologically and in terms of interpreting the results of experiments. Response predictability can be thought of as a form of ecosystem reliability, such that changes in response predictability will affect the consistency of the level of ecosystem performance (Naeem 1998). Response predictability can therefore be used as an indicator of the resistance of ecosystems to human-induced environmental changes (Naeem & Li 1997; Morin & McGrady-Steed 2004; Carpenter & Brock 2006), where a change in response predictability indicates low resistance. Response predictability may also be an important metric for assessing potential for recovery following global change. For example, drivers such as species invasions that result in

reductions in beta-diversity or biotic homogenization (Olden et al. 2004) may reduce opportunities for re-colonization of native species.

We conducted a meta-analysis to determine how response predictability is affected by species extinction and by four additional human-induced environmental changes (species invasions, nutrient addition, temperature increase, and habitat loss/fragmentation). These environmental changes have all been identified as major drivers of biodiversity decline. We further determined whether response predictability differed in aquatic versus terrestrial habitats and between producers and consumers.

We developed three major predictions for how response predictability would be affected by the specific type of global change driver and across different habitat types and trophic roles. First, biotic drivers, which directly affect species interactions, will lead to higher magnitude changes in response predictability than abiotic disturbances (Van Cleve et al. 1991; Chapin et al. 2000). Second, potentially stronger species interactions and shorter turnover times in aquatic systems compared to terrestrial systems will lead to higher magnitude change in response predictability in aquatic systems (Shurin et al. 2002). Third, drivers that involve species at the base of food webs will lead to higher magnitude changes in response predictability than drivers that involve higher trophic levels (Brett & Goldman 1997; Marczak et al. 2007).

The five global change drivers included here may also result in differences in the direction of the response. Species-poor communities are more temporally variable than species-rich communities (Jiang & Pu 2009). As spatial and temporal variability are typically highly correlated (Wiens 1989), it is likely that species removals will lead to decreases in response predictability. Species invasions have been shown to lead to widespread biotic homogenization (Rahel 2002), suggesting that species invasions might increase response predictability. Nutrient addition is often associated with temporal destabilization of both population and community properties; thus, is likely to lead to decreases in response predictability. Habitat loss/fragmentation is a primary cause of species loss; thus, may lead to decreases in response predictability through its negative effect on diversity. Habitat loss/fragmentation may also lead to increases in response predictability, as smaller patches are more likely to be similar to each other in composition than larger patches. Finally, increases in temperature could lead to either

increases or decreases in response predictability. Increased response predictability could result as species respond more similarly under stressful conditions due to weaker inter- and intra-species interactions (Van der Putten 2010). However, higher temperatures might also lead to decreases in response predictability, particularly if local extinctions occur and species ranges change (Pounds et al. 1999; Wake & Vredenburg 2008).

4.3   Methods

We performed a literature search for empirical studies of the diversity and/or abundance responses to species extinction or one of the four drivers mentioned above. We found papers using both the ISI Web of Knowledge database and by reviewing the references of appropriate papers. A total of 91 papers that included 345 experimental manipulations were included in the final analysis. All papers reported a mean measure of abundance, biomass, density, species diversity, or species richness in both a control and impacted treatment. No significant difference was found between responses for species richness and diversity or between abundance, density, or biomass (Figure C.1). As a result, we grouped these measures into two main response variables to assess response predictability (RP). The diversity group ($RP_{diversity}$) included responses for species richness, number of species, as well as various measures of abundance weighted diversity (e.g. H'). The abundance group ($RP_{abundance}$) included numerical counts (abundance, density) and biomass.

   We categorized habitat loss/fragmentation, temperature increase, and nutrient addition as abiotic drivers of change and species invasions and removals as biotic drivers of change. All studies had either two or more replicates per treatment, and the standard error of the response variable for each treatment was either reported in the paper (33 papers), or could be easily measured from the figures (58 papers). Papers where the standard error bar values displayed in the figures were too difficult to extrapolate were not included in our analysis. For studies that manipulated drivers over a range of intensities, we used the average value across all treatments rather than including each response.

   We followed strict guidelines in choosing the types of studies to be included in the analysis. For the temperature increase category we only included studies that increased temperature *per se* (eg. Chapin et al. 1995). Studies that combined other climate change

effects, such as altered light and precipitation, with increases in temperature were not included (e.g., Zhou et al. 2006). Additionally, observational studies which compared natural communities growing in areas that differ in ambient temperature (eg. Kennedy 1996) were not included. For nutrient addition we included studies that enriched the experimental community with nitrogen (e.g., Bonanomi et al. 2009), phosphorus (e.g., Cherwin et al. 2008), or a fertilizer solution containing one or both of these nutrients (e.g., Lindberg & Persson 2004). For habitat loss and fragmentation we included studies that fragmented experimental plots (e.g., Gonzalez & Chaneton 2002) or those that compared communities present in control sites to those that had been clear cut or logged (e.g., Dumbrell et al. 2008; Biswas & Mallik 2010). We did not include studies that examined abundance and diversity in different sized patches without actually fragmenting the patches experimentally, nor did we include studies that combined corridor effects with fragmentation (e.g., Rantalainen et al. 2004). The only studies included in the species removal category were those in which a single species, or group of species, were removed from the experimental community. We did not include studies that created communities based on biodiversity gradients (e.g., Symstad et al. 1998) or those that decreased the abundances of species without completely removing them. Finally, for species invasions we only included studies in which a non-native species, or group of non-native species, was added to an established community. We did not include studies that examined the effects of removing non-native species from previously invaded communities (eg. Ostertag et al. 2009).

We converted standard errors to variance and calculated response ratios [RR= ln (impacted/control)]. The response ratio is a common effect size measure in ecological meta-analyses (Hedges et al. 1999). Response ratios that are significantly greater or less than zero indicate a larger change in the response between the control and impacted treatments. The direction of change indicates whether the impacted treatment had a positive (decreased response predictability) or negative (increased response predictability) response relative to the control treatment. Response ratios (RR) were calculated for the mean response in diversity and abundance for both the control and disturbed groups across all studies (see Figure 4.1) and for a standardized measure of the variance: the ratio of the lnRR variance and the mean lnRR (the variance-mean ratio).

We calculated the effect sizes using average values of the response ratios. We determined significant differences from zero using t-tests and significant differences between categories using one-way analysis of variance. A common practice in meta-analyses is to weigh the effect sizes based on standard error, so that studies with less variance have a higher weighting in the analysis. Since our study uses variance:mean ratios as the measure of effect size and we did not want variance to be a factor in how the effect sizes were weighted, we did not weight effect sizes.

Studies were grouped based on the response variable, either abundance or diversity, for all factors. Five factors were used in the meta-analysis:

1. Mean vs. Variance: 1) the total mean effect size, 2) the total variance:mean effect size (RP).
2. Driver type: drivers were grouped into abiotic (habitat loss/fragmentation, temperature increases, nutrient addition) or biotic (invasive species, species removal), and further grouped into one of the five specific driver categories: habitat loss/fragmentation, nutrient addition, temperature increase, invasion by a non-native species, and removal of a species.
3. Habitat: whether the study was conducted in an aquatic or terrestrial system. Habitat was further separated into the different driver types.
4. Response trophic role: whether the species, or group of species, being measured in the study were producers or consumers. Response trophic role was further separated into the different driver types.
5. Effect trophic role: whether the species invading or being removed from the system was a producer or consumer.

4.4   Results

4.4.1   Effects On Response Predictability

Human-induced environmental changes had a strong negative effect on mean diversity (p=0.016) and mean abundance (p=0.013), showing significantly lower diversity and abundance in impacted treatments relative to the control across all driver types (Figure 4.1A). In contrast to these consistent changes in community structure for average values, response predictability for both $RP_{abundance}$ and $RP_{diversity}$ did not differ significantly between control and impacted treatments (Figure 4.1B; Table 4.1). This lack of an overall change in response predictability was due to the presence of a strong bimodal pattern with 42 negative and 56 positive $RP_{abundance}$ effect sizes, and 16 negative and 13 positive $RP_{diversity}$ effect sizes. Despite these directionally different responses within $RP_{abundance}$ and $RP_{diversity}$, $RP_{abundance}$ showed a trend towards a decrease in response predictability in impacted treatments and $RP_{diversity}$ showed a trend towards an increase in response predictability in impacted treatments (Figure 4.1; Table 4.1). The mean effect size for $RP_{abundance}$ and $RP_{diversity}$ differed significantly (p=0.049) with $RP_{abundance}$ showing reductions and $RP_{diversity}$ increases in RP with global change drivers.

Across all global change drivers, $RP_{diversity}$ was significantly greater in aquatic systems than in terrestrial systems (p=0.001) while $RP_{abundance}$ did not differ significantly between the two habitat types (p=0.534; Table 4.2). Both $RP_{abundance}$ and $RP_{diversity}$ did not significantly differ between producer and consumer species across all drivers ($RP_{abundance}$ p=0.88; $RP_{diversity}$ p=0.36; Table 4.2).
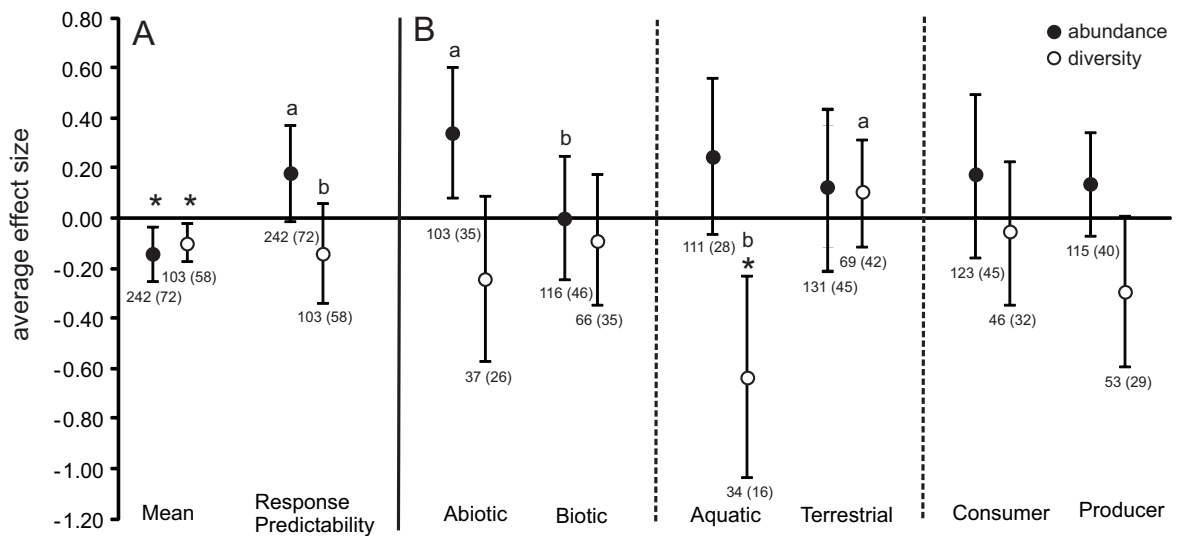
Figure 4.1: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between drivers, habitats, and trophic roles. The values below each point represent the number of results included in the analysis and, in parentheses, the number of papers that those results were taken from. Values that significantly differ from zero (p=0.05) are indicated with an asterisk, and letters that do not match indicate significant differences between two values (p=0.05). (A) the average response ratios for the mean and response predictability across all drivers (B) the average response ratios for response predictability for abiotic versus biotic drivers of change, habitat type, and trophic role of affected species.

Table 4.1: Sample sizes, effect sizes, and t-test p-values for each of the comparisons included in the meta-analysis for response predictability in abundance and diversity.

	Abundance			Diversity		
	n	Mean effect size	P	n	Mean effect size	P
Across all disturbances (fig. 1):						
Overall mean response ratio	242	.14	.004	103	.096	.009
Overall response predictability	242	.183	.17	103	−.141	.24
Abiotic	103	.342	.01	37	.239	.147
Biotic	116	.002	.99	66	−.086	.513
Aquatic	111	.249	.115	34	−.632	.003
Terrestrial	131	.127	.304	69	.101	.348
Consumer	123	.169	.305	46	−.058	.688
Producer	115	.139	.184	53	−.291	.056
Disturbance types (fig. 2):						
Habitat loss	24	.45	.328	20	−.034	.871
Nutrient addition	74	−.031	.869	36	−.393	.055
Invasive species	54	.286	.127	19	−.211	.335
Species removal	52	.225	.179	15	.306	.069
Temperature increase	36	.241	.326	4	−.755	.329
Habitat with disturbance type (fig. 3):						
Aquatic:						
Habitat loss	1	−1.372	...	1	−2.086	...
Invasive species	69	.071	.718	23	.595	.036
Nutrient addition	14	1.252	.005	4	.767	.231
Species removal	24	−.077	.775	5	.268	.322
Temperature increase	3	2.82	.211	1	−1.3	...
Terrestrial:						
Habitat loss	23	.529	.265	19	.074	.693
Invasive species	7	−1.038	.066	13	−.036	.894
Nutrient addition	40	−.051	.785	15	−.063	.785
Species removal	28	.484	.021	19	.456	.02
Temperature increase	33	.006	.973	3	−.572	.582
Trophic role of response species with disturbance type (fig. 4):						
Consumer:						
Habitat loss	20	.606	.258	17	.002	.995
Invasive species	45	−.24	.337	12	−.046	.891
Nutrient addition	22	.364	.365	10	.245	.416
Species removal	27	.229	.347	7	.047	.899
Temperature increase	9	.582	.519	0	...	...
Producer:						
Habitat loss	4	−.334	.668	3	−.235	.651
Invasive species	31	.273	.336	24	−.567	.029
Nutrient addition	32	.233	.159	9	−.174	.618
Species removal	21	−.096	.633	13	.267	.228
Temperature increase	27	.127	.443	4	−.755	.329
Trophic role of invasive or removed species (fig. 5):						
Consumer:						
Invasive species	62	.092	.671	7	.099	.477
Species removal	36	−.015	.943	9	.007	.803
Producer:						
Invasive species	14	−.573	.099	14	−.392	.008
Species removal	16	.764	.007	7	.531	.01

Table 4.2: ANOVA results for each of the main effects and interaction effects included in the meta-analysis for response predictability in abundance and diversity.

	SS	df	MS	F	P
Abundance:					
Disturbance type	5.97	4	1.49	.64	.63
Abiotic vs. biotic	10.75	1	10.75	4.7	.03
Aquatic vs. terrestrial	.904	1	.905	.389	.534
Consumer vs. producer	.05	1	.05	.02	.88
Diversity:					
Disturbance type	8.9	4	2.23	2.18	.08
Abiotic vs. biotic	.78	1	.78	.71	.4
Aquatic vs. terrestrial	11.34	1	11.34	11.45	.001
Consumer vs. producer	.94	1	.94	.85	.36
Abundance:					
Habitat × disturbance	43.66	4	10.92	5.08	.0006
Trophic × disturbance	10.53	4	2.63	1.14	.34
Diversity:					
Habitat × disturbance	2.2	4	.55	.57	.69
Trophic × disturbance	2.42	4	.81	.75	.52

4.4.2 Driver Type

Due to strong habitat differences, $RP_{abundance}$ and $RP_{diversity}$ did not show significant changes for any of the driver types (Figure 4.2); however, two trends are of significant interest. Species invasions led to a marginally significant increase in $RP_{diversity}$ (p=0.055) and species removals led to a marginally significant decrease in $RP_{diversity}$ (p=0.069). Neither of these drivers led to changes in $RP_{abundance}$. $RP_{abundance}$ and $RP_{diversity}$ both did not differ between each of the five drivers ($RP_{abundance}$ p=0.63; $RP_{diversity}$ p=0.08). $RP_{abundance}$ was significantly lower following abiotic drivers of change than biotic drivers of change (p=0.03) while $RP_{diversity}$ did not significantly differ between abiotic and biotic drivers (p=0.4).

Figure 4.2: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between five global change drivers. The values below each point represent the number of results included in the analysis and, in parentheses, the number of papers that those results were taken from. Values that significantly differ from zero (p=0.05) are indicated with an asterisk, and letters that do not match indicate significant differences between two values (p=0.05).

58

4.4.3 Driver X Habitat

When global change drivers were separated according to habitat, a number of significant changes in RP were observed. In aquatic habitats, nutrient addition decreased $RP_{abundance}$ (p=0.005) and invasive species increased $RP_{diversity}$ (p=0.036; Figure 4.3). In terrestrial habitats, species removal decreased both $RP_{abundance}$ (p=0.021) and $RP_{diversity}$ (p=0.02). $RP_{abundance}$ differed significantly between drivers when separated by habitat (p=0.0006). Post-hoc analysis showed that this difference was driven by a significant difference in temperature increase between aquatic and terrestrial systems. However, this difference was likely due to low sample sizes within all the terrestrial study comparisons. $RP_{diversity}$ did not differ between drivers when separated according to habitat (p=0.69).

Figure 4.3: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between driver-habitat combinations. The values below each point represent the number of results included in the analysis and, in parentheses, the number of papers that those results were taken from. Values that significantly differ from zero (p=0.05) are indicated with an asterisk, and letters that do not match indicate significant differences between two values (p=0.05).

59

4.4.4 Driver X Trophic Role

When separated according to the trophic role of the species for which the response was measured, the only significant change in RP was for producers, which showed an increase in $RP_{diversity}$ with species invasions (p=0.029; Figure 4.4). When separated according to the trophic role of the invading or removed species, studies involving producers had stronger effects than studies involving consumers (Figure 4.5). There was a significant decrease in $RP_{abundance}$ (p=0.007) and $RP_{diversity}$ (p=0.01) for producer removals. Invasions by producers led to marginal increases in $RP_{abundance}$ (p=0.099) and $RP_{diversity}$ (p=0.08). None of the five global change drivers differed significantly from one another for either $RP_{abundance}$ or $RP_{diversity}$ when drivers were separated according to trophic role ($RP_{abundance}$ p=0.34; $RP_{diversity}$ p=0.52).
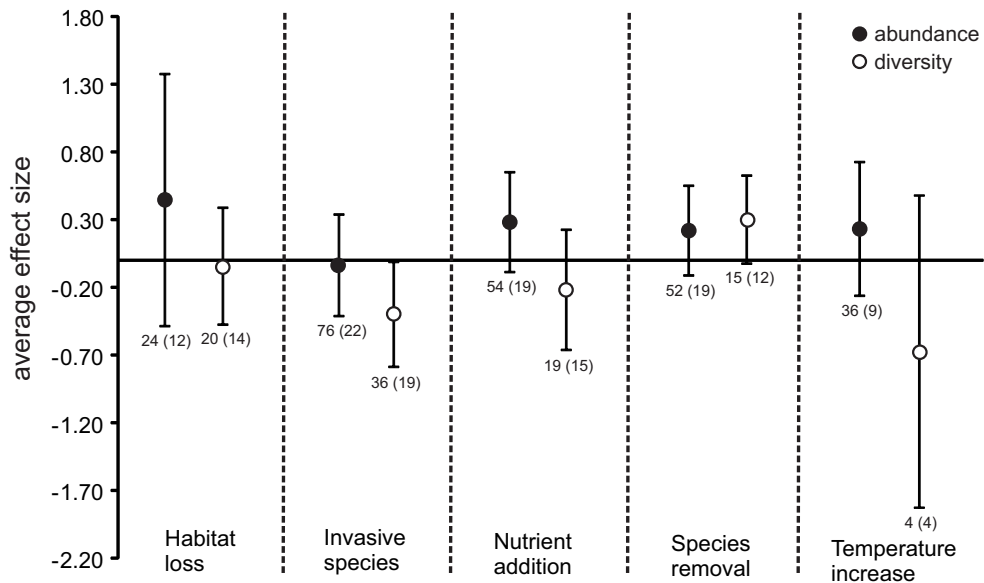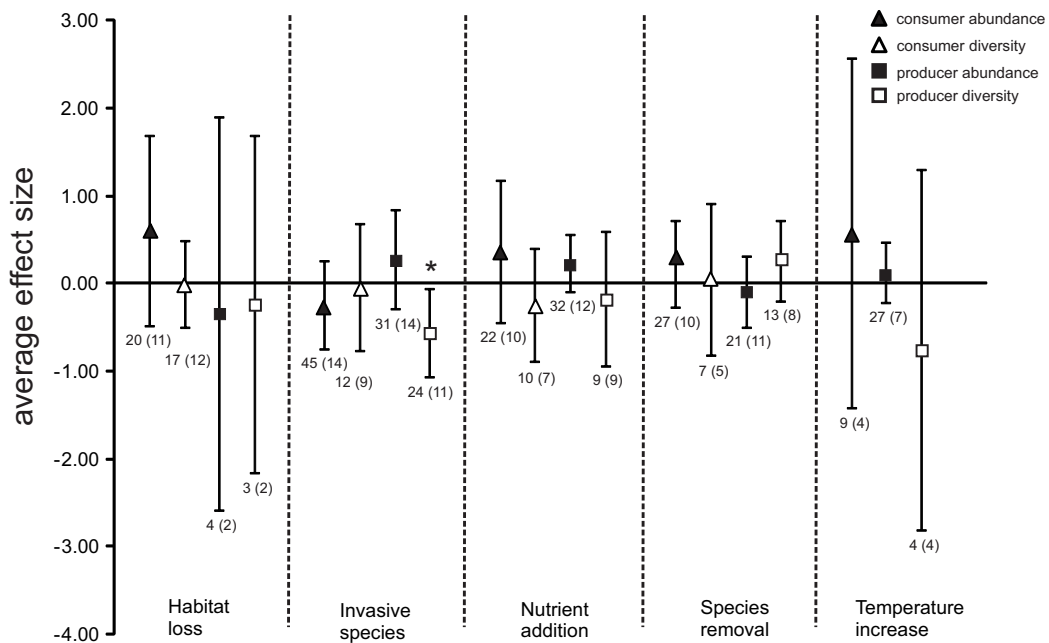

Figure 4.5: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between driver-trophic role combinations. The values below each point represent the number of results included in the analysis and, in parentheses, the number of papers that those results were taken from. Values that significantly differ from zero (p=0.05) are indicated with an asterisk, and letters that do not match indicate significant differences between two values (p=0.05).
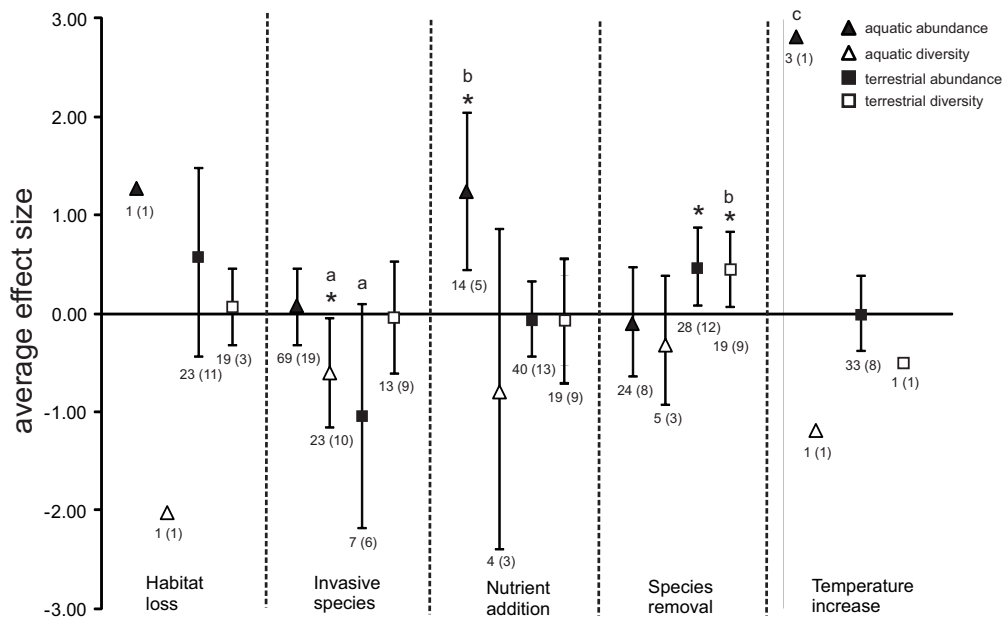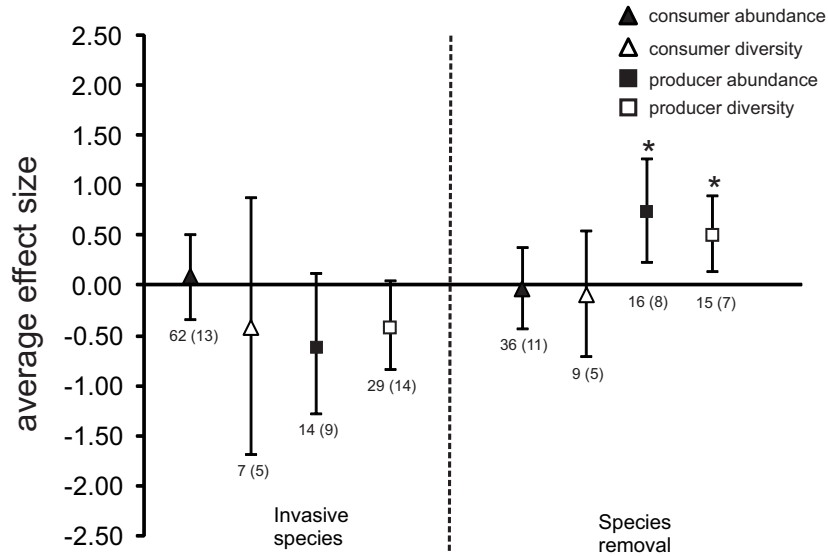
Figure 4.6: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between invading or removed species trophic roles. The values below each point represent the number of results included in the analysis and, in parentheses, the number of papers that those results were taken from. Values that significantly differ from zero (p=0.05) are indicated with an asterisk, and letters that do not match indicate significant differences between two values (p=0.05).

4.5   Discussion

Response predictability is an important ecological response to environmental change and has major implications for understanding how global change drivers affect ecological communities. It can also be used as a metric when assessing the potential for ecosystem recovery and for interpreting the results of experiments.

Average values of diversity and abundance decreased across all driver types showing a significant widespread reduction in the complexity of communities following human-induced environmental change (Figure 4.1). In contrast to this clear negative effect of global change drivers on average values, which we do not consider here further, we did not detect a significant difference in response predictability for either abundance or diversity across all driver types (Figure 4.1). This lack of an overall effect of global change drivers on response predictability was due to the highly dichotomous nature of the response ratios, which included 169 negative and 175 positive response ratios, showing that global change drivers can both increase and decrease response predictability. This strong dichotomy arose due to the opposite effects of species invasions, which led to

increased response predictability, versus nutrient addition and species removal, which led to decreases in response predictability.

Whether community structure converges (response predictability increases) or diverges (response predictability decreases) following environmental change may be partly due to the role that deterministic versus stochastic processes play in restructuring communities (Houseman et al. 2008; Chase & Myers 2011; Myers & Harms 2011). For example, Chase (2007) showed variance in species composition between replicate ponds decreased (became more predictable) in ponds exposed to drought compared to ponds not exposed to drought. Chase (2007) attributed this increase in similarity to an increase in deterministic processes structuring the drought-affected communities. While both deterministic and stochastic processes interact to structure communities (Chase 2007), the importance and strength of each process may differ based on different environmental stresses. Deterministic, or niche-assembly, processes, where community structure results from the niche requirements of species, may be associated with increases in response predictability. On the other hand, stochastic, or dispersal assembly, processes, which structure communities through variations in dispersal and demographic stochasticity, may be associated with decreases in response predictability (Myers & Harms 2011).

The decrease in diversity response predictability caused by removals, and increase caused by invasions that we found suggest that during community restructuring species invasions may lead to a stronger role for deterministic processes, while species loss may lead to stronger roles for stochastic processes. For example, the increase in response predictability we observed for species invasions is suggestive of the reductions in beta-diversity or biotic homogenization that is considered a major consequence of non-native species invasions (McKinney & Lockwood 1999; Rahel 2002; Olden et al. 2004). In contrast, the decrease in diversity response predictability, and thus divergence in composition, following species removals suggests that removing species may increase the importance of stochastic processes. That species loss can increase variability within ecosystems has been widely documented (Loreau et al. 2000; Ives & Carpenter 2007; Campbell et al. 2011); however, the majority of studies have focused on temporal variability. Those studies that have focused on variability among replicates have found a trend of decreased variability (increased response predictability) in more species-rich

treatments (Naeem & Li 1997), suggesting that response predictability is correlated with species richness. While species richness may be an important determinant of response predictability within experiments, we found no correlation between species richness and response predictability overall or within any of the driver types (Figure A.2).

The potential for a stronger role for deterministic processes following species invasions and stochastic processes following species removals could lead to differences in how communities re-structure following environmental change. Invasions appear to lead to greater similarity in diversity among replicates whereas species loss leads to divergence in community structure. Whether an invading species will be successful or not depends on the niche requirements of the species as well as competition for resources or space with local species. In contrast, species loss opens space in a community or increases availability of resources. Thus, the relative importance of the roles of deterministic and stochastic processes operating following species invasion and loss should shift based on the type of biotic disturbance. While we observed a strong effect of direct species removal on response predictability, we did not observe a significant effect of temperature or habitat loss/fragmentation on response predictability. These drivers of change affect many aspects of ecosystem functioning as well as lead to changes in species richness. Interestingly, we did not observe a significant change in response predictability for temperature increase or habitat loss. The most likely explanation for the lack of significant effects of temperature and habitat loss on response predictability is that the outcome of these drivers differs strongly across habitats, trophic roles, and environmental conditions. Broad ranges in effect sizes were observed for both of these drivers (Figure 4.1). Furthermore, for temperature (n=3) and habitat loss (n=1) in aquatic systems in particular, fewer appropriate studies were included in our meta-analysis than for the other drivers. Thus, it is likely that a finer level of categorization such as across biomes (e.g. Sala et al. 2000) is necessary to determine how response predictability is affected by habitat loss or temperature. However, based on our results for species invasions and species loss it is likely that if temperature increase or habitat loss affects the numbers of species in the system, by increasing rates of invasions or rates of species loss, an increase or decrease in response predictability may result based on how diversity is affected.

That stochastic processes might play a stronger role in restructuring communities following nutrient addition is particularly intriguing. We observed a strong decrease in response predictability in abundance with nutrient addition in aquatic communities. That increased productivity often drives decreases in predictability has long been recognized (Warwick & Clarke 1992; Chase & Leibold 2002). Slight variations in initial species composition or stochastic priority effects that become magnified with fertilization are two primary mechanisms that have been suggested to underlie this pattern (Steiner & Leibold 2004; Soininen et al. 2005; Houseman et al. 2008). These mechanisms highlight the importance of stochastic processes in community re-structuring following nutrient addition.

We predicted that biotic global change drivers (species invasions and extinctions) would lead to higher magnitude changes in response predictability than abiotic drivers (nutrient addition, temperature increase, habitat loss), as biotic drivers have a more direct and potentially stronger impact on species interactions (Van Cleve et al. 1991; Chapin et al. 2000). Support for this prediction was mixed. Across habitat and trophic categories, abiotic global change drivers led to significant decreases in abundance response predictability. Abundance response predictability was also significantly lower following abiotic drivers than biotic drivers (Table 4.2). As discussed previously, this lack of effect for biotic global change drivers was due to the strongly dichotomous trends in response predictability for species invasions and species removals. When separated by driver type, only species invasions and species removals led to changes in response predictability; however, these effects were not consistent across habitat types (Figures 4.2 and 4.3). The significant decrease in response predictability for abiotic drivers was driven by the results from the aquatic nutrient addition studies as no significant changes in response predictability were observed for either habitat loss or temperature increase.

That changes in response predictability can differ for similar disturbances in different habitats was strongly supported by our results. Aquatic and terrestrial systems differ in terms of food web structure and ecosystem properties. Terrestrial systems are generally more productive and complex with shorter food chain lengths, while aquatic systems have shorter timescales and potentially stronger interactions between species (Shurin et al. 2002). These differences suggest that aquatic and terrestrial systems will

differ in at least some aspects of their response to different environmental changes. In support of this prediction we found a significant increase in response predictability in diversity in aquatic communities across all driver types. This trend was not observed for terrestrial systems (Figure 4.1, Table 4.1). Diversity response predictability was also significantly greater in aquatic systems than in terrestrial systems across all drivers (Table 4.2). Therefore, across all global change drivers, aquatic systems appear to be more susceptible to changes in response predictability than terrestrial systems.

A similar trend was also observed for species invasions, with an increase in response predictability in diversity observed for invasions in aquatic but not terrestrial habitats. This suggests that biotic homogenization resulting from invasions may be more prevalent in aquatic ecosystems (Qian & Guo 2010). In contrast, in terrestrial systems, invasions increased response predictability in abundance. While this latter result could be an artifact of low sample size (n=7), mechanisms underlying invasion success have been shown to differ between terrestrial and aquatic habitats. For example, positive diversity-invasibility relations are often observed at larger scales in terrestrial habitats (Levine 2000) and greater evolutionary differences between native and non-native species have been proposed as one reason why aquatic habitats are more easily invaded than terrestrial habitats (Mooney & Cleland 2001).

Broad habitat differences were also observed for species removals. When separated by habitat, the trend of decreased predictability following a species removal was only significant for terrestrial systems. The question of why species removals would decrease response predictability in terrestrial systems but not in aquatic systems is of significant interest. It suggests that, in general, terrestrial systems may be destabilized by species loss more so than aquatic systems. It has previously been suggested that the stabilizing effects of diversity may differ in terrestrial versus aquatic systems (Jiang & Pu 2009). Studies conducted in terrestrial systems typically manipulate and measure responses in plant guilds while studies conducted in aquatic systems manipulate and measure responses in consumer guilds.

The one other global change driver for which a habitat difference was observed was for nutrient addition, which significantly decreased in response predictability in abundance only in aquatic systems. We attribute this difference in habitat response to

more pronounced effects of nutrient enrichment in aquatic systems due to the shorter timescales and higher rates of herbivory, which allow nutrients to recycle faster in aquatic as compared to terrestrial systems (Shurin et al. 2002).

Along with habitat differences, we also found that trophic status had a major effect on whether or not response predictability changed significantly following human-induced environmental changes (Figure 4.1). While neither abundance nor diversity response predictability differed significantly between producer and consumer species across all global change drivers (Table 4.2), we found significant changes in response predictability according to trophic status for specific drivers. When considering the producer-consumer distinction in terms of the response to global change drivers our results suggest that biotic homogenization following species invasions is particularly strong for producers. This is because response predictability in producer diversity was the only metric to decrease significantly following species invasions. When considering whether the invasive species or species removed was a producer or consumer we found that only invasions or removals of producers led to significant changes in response predictability. Producer invasions led to significant increases in diversity response predictability, while producer removals led to significant decreases in both abundance and diversity response predictability. These results suggest that alterations at the base of the food web may lead to more consistent effects than environmental changes that more strongly impact consumer species.

The meta-analysis presented here is the first attempt to summarize how response predictability changes following human-induced environmental change in ecological communities. Many additional patterns and trends not discussed here may be of considerable interest in understanding how global change affects response predictability. One pattern that we did not discuss in detail is why some drivers of global change affect response predictability in abundance only, others diversity only, and some both. For example, species removals decreased both abundance and diversity response predictability in terrestrial systems, while the effect of species invasions was limited to diversity in aquatic systems and abundance in terrestrial systems. These types of differences provide potentially important information for predicting the consequences of environmental changes. Likewise, the implication of different directional changes in response predictability in assessing the potential for ecosystem recovery (Benayas et al.

2009) holds considerable promise. The directional differences in response predictability observed suggest that effective methods to manage ecosystems recovering from species loss may be very different from management needed following species invasions. This is due to differences in post-disturbance community assembly processes and the reduction in spatial variability in diversity that would inhibit natural recolonization. Finally, the strong effects we observed for response predictability in three out of five global change drivers, and the overall increase in response predictability across all drivers in aquatic systems, reinforces the importance of addressing changes in variance along with average values when interpreting the results of empirical global change studies. In conclusion, response predictability is a useful metric that can provide a wide range of information on how environmental change affects ecological communities that is overlooked when considering average values alone.

4.6   Acknowledgements

CHAPTER 5

IMPACTS OF HUMAN-INDUCED ENVIRONMENTAL CHANGES ON ECOSYSTEM PROCESSES

5.1   Abstract

Human activity is known to threaten the processes that drive the functioning of ecosystems, yet there is uncertainty in regards to the magnitude and direction of ecosystem process responses to global change. We conducted a global meta-analysis to estimate the effects of five human-induced environmental changes on several key ecosystem processes (primary production, carbon storage, nitrogen mineralization, decomposition, and respiration). Our results show that, in contrast to the significant negative impact of species invasions on local biodiversity, species invasions do not have consistently strong effects on several ecosystem processes. Instead, ecosystem processes are primarily influenced by warming and nutrient addition. We also observed no overall effect of warming on primary production, yet strong effects on decomposition (12% increase) and respiration (10% increase), suggesting that warming may lead to a net release of carbon to the atmosphere. Our results demonstrate that the environmental stressors most important in driving change to ecosystem processes differ from those that drive local biodiversity change. Predicting the influence of human-induced environmental changes on ecosystem functioning will require a better understanding of the extent to which stressors directly impact ecosystem processes and indirectly impact processes through biodiversity change.

5.2   Introduction

The relationship between biodiversity loss and the functioning of ecosystems has been an area of substantial research interest over the past decades (Cardinale et al. 2012). With the development of the biodiversity-ecosystem function field of study, numerous experiments have provided undeniable evidence that biodiversity loss affects the ecological processes that control the functioning of ecosystems, such as primary production, decomposition, carbon storage, and nutrient cycling (Naeem et al. 1994; Tilman et al. 1997; Hooper et al. 2005). The biodiversity-ecosystem function relationship is often used to predict the consequences of species loss (Mascaro et al. 2012). However, while species loss at the global scale is well recognized and is an area of critical conservation concern (Barnosky et al. 2011), it is at the local-scale that biodiversity change is expected to have the most impact on ecosystem processes (Loreau et al. 2001; Pasari et al. 2013).

Currently, the magnitude and direction of local biodiversity change occurring on Earth today is an issue of contention (Gonzalez et al. 2016). Recent biodiversity change syntheses have revealed that, at the local scale, biodiversity may not be declining (Vellend et al. 2013, Dornelas et al. 2014). Other syntheses have shown that the magnitude of local biodiversity change is dependent on drivers of change, and can vary across trophic levels and biomes (Murphy & Romanuk 2014). Local increases in species richness are well documented in human impacted ecosystems and result from exotic species introductions outnumbering native species extinctions (Sax & Gaines 2003). While the introduction of non-native species may maintain or even increase species richness, invaders are unlikely to fill the same roles of the native species they replace, and thus, ecosystem processes are likely to still be affected. The uncertainty in the magnitude of local-scale biodiversity change occurring from human activity suggests that it may be more appropriate to directly examine how the global change drivers that impact biodiversity will affect ecosystem processes, rather than making inferences about the potential effects from the biodiversity-ecosystem function relationship.

Prior research has shown that global change drivers can have diverse effects on ecosystem processes. For instance, invasions are often associated with increased primary production and carbon storage (Jackson et al. 2002; Wolkovich et al. 2010), while the

effect of nutrient addition on carbon storage has remained controversial with some studies reporting decreases (Zeng et al. 2010) and others reporting no effect (Lu et al. 2011). Acidification has been shown to reduce decomposition rates, while increased temperatures are generally thought to increase decomposition, respiration, and nitrogen mineralization, which can result in a positive feedback to climate change (Rustad et al. 2001; Schuur et al. 2009; Allison et al. 2010). The effects of these global change drivers on ecosystem processes have also been shown to differ across habitats and biomes. For example, the impacts of climate change on productivity can differ widely among the Earth's biomes (Zhang et al. 2013; Silva & Anand 2013).

Here, we use a meta-analysis of published data to explore the extent to which five human-induced environmental changes impact five ecosystem processes. Numerous meta-analyses have been conducted examining the effects of different human activities on ecosystem processes (Rustad et al. 2001; Luo et al. 2006; Lecerf & Chauvet 2008; Liao et al. 2008; Janssens et al. 2010), yet these meta-analyses typically focus on one type of environmental change, ecosystem process, species, or biome.

We focus our analysis on five ecosystem processes: carbon storage, decomposition, nitrogen mineralization, primary production, and respiration. These processes drive many of the ecosystem services that provide immense benefits to humanity, such as food production, carbon sequestration, and climate regulation. We test the magnitude and direction of change in these ecosystem processes following five major drivers of ecosystem change (Vitousek et al. 1997). These include: warming, N addition, NP addition, species invasion, and acidification. In addition to the individual effects, we also test the magnitude of ecosystem process responses to the combination of warming and nutrient addition.

5.3   Methods

5.3.1 Selection Criteria

We compiled the dataset by carrying out a literature search for studies that reported change in ecosystem processes in a control and impacted treatment for one of the five global change drivers outlined above. Other human activities, such as, overexploitation,

land transformation, and pollution, can contribute to altered ecosystem functioning. We chose these five drivers of change, as they are the most common drivers examined in empirical ecosystem function research, and this selection allows us to make comparisons to local biodiversity responses of the same drivers (Murphy & Romanuk 2014). Likewise, while numerous other ecosystem processes are critical to the functioning of ecosystems and may also be influenced by human-induced environmental changes, we focused specifically on five ecosystem processes that, along with playing an important role in ecosystem functioning, are among the most commonly reported in empirical global change studies.

We performed a literature search using the ISI Web of Science database of the following research areas: "environmental sciences", "ecology", "biodiversity conservation", "marine freshwater biology", and "soil science". We used the following search expressions: "ecosystem function" OR "ecosystem process" OR "carbon storage" OR "decomposition" OR "nitrogen mineralization" OR "primary production" OR "respiration" AND ("acidification" OR "invasi* species" OR "eutrophication" OR "nutrient add*" OR "climate change" OR "experiment* warm*" OR "increase* temperature"). We also reviewed the references of relevant published meta-analyses for suitable studies. A final search of the literature was completed on 3 November 2014. We included studies that experimentally manipulated drivers or observational studies that compared an impacted area with a control (un-impacted) area. All papers reported a mean measure of one or more of the five ecosystem processes and a corresponding error measure in both an impacted and control treatment. Values were either given in the paper or were extracted from figures using GetData Graph Digitizer software. We took data from the final sampling date for studies that measured change in ecosystem processes over a period of time.

We followed a strict set of guidelines in choosing the types of studies to be included in the analysis. For the acidification category, we included studies that decreased the pH of the treatment using CO2 aeration or the addition of acid. We also included observational studies that compared measures of ecosystem processes in an anthropogenically acidified habitat and a reference habitat. Studies that measured ecosystem processes in naturally acidic versus neutral areas were not included. We chose

to only include aquatic acidification studies for this category. For species invasions, we included studies in which a non-native species was added (intentionally or unintentionally) to a habitat. We also included observational studies that examined an uninvaded site with an invaded site. For nutrient addition, we included studies that enriched the experimental communities with nitrogen or a nitrogen-phosphorus combination. For warming, we included studies that increased temperature of the experimental community. We excluded studies where the increase in temperature was greater than 10°C. We did not include warming studies that compared ecosystem processes in natural ecosystems differing in ambient temperature. Finally, we included studies that combined warming and nutrient addition (grouping together both N and NP-addition studies).

We included various measures of the ecosystem processes for each factor. Responses were classified according to how they were described by the authors of the original studies. For carbon storage we included measures of soil/sediment carbon, dissolved carbon, carbon content of primary producers, microbial carbon, and total ecosystem carbon. For decomposition we included measures of decay/breakdown rate, decomposition constant, or mass loss. For studies that reported a measure of mass remaining we converted the sign of the effect size to represent mass loss. For nitrogen mineralization we included measures of nitrogen mineralization rate. For primary production we included measures of primary producer biomass and primary production. For respiration we included measures of ecosystem, microbial, autotrophic and soil/sediment respiration rates.

5.3.2 Data Analysis

To analyze the responses of ecosystem processes to global change drivers we performed weighted random effects meta-analyses using the *metafor* package in R (Viechtbauer 2010). We considered a random effects analysis, which assumes that effect sizes will exhibit random variation among studies, to be more appropriate than a fixed effects analysis as the studies included in our dataset vary widely in both methodology and biological factors. We used the standard equation for the response ratio (RR) as the effect size for the analyses to compare the mean ecosystem processes between impacted ($\bar{X}_i$) and control conditions ($\bar{X}_c$). The response ratio is calculated as:

$$RR = ln\left(\frac{\overline{X}_i}{\overline{X}_c}\right)$$

The response ratio is a common effect size measure in ecological meta-analyses (Hedges et al. 1999). Response ratios that are significantly greater or less than zero indicate a larger change in the ecosystem process measure between the control and impacted treatments, with the direction of change indicating whether the impact increased or decreased the ecosystem process relative to the control treatment. We converted effect sizes to percentage of change using the base of the natural logarithm:

$$\% = (e^{RR} - 1) \times 100$$

The independent responses in the analyses were weighted according to their sample variance to account for the difference in statistical precision between individual studies (Hedges et al. 1999). Greater weight is given to studies whose estimates have a smaller standard error, thus a greater precision. Variance for each response was calculated using as:

$$v = \frac{S_i^2}{n_i \overline{X}_i^2} + \frac{S_c^2}{n_c \overline{X}_c^2}$$

We used 95% confidence intervals to determine significant increases or decreases in the effect sizes, and to compare the effects between different categories within a factor. We used general linear models to test the magnitude of temperature change and nitrogen addition on ecosystem process responses. We also examined the relationship between study duration and effect size to verify that differences in magnitudes of responses were not being driven by the duration of the study. When analyzing differences in warming responses between habitats, we grouped together processes that contribute to carbon uptake (primary production and carbon storage) and processes that contribute to carbon efflux (decomposition and respiration), to increase the sample sizes for each habitat.

5.4   Results

Our literature search returned 270 suitable publications published between 1988-2014 from which we calculated 1268 ecosystem process responses to human-induced environmental changes.

Warming and nutrient addition had the strongest effects on several ecosystem processes (Figure 5.1). Warming resulted in a significant 62% increase in nitrogen mineralization (n = 14), 12% increase in decomposition (n = 47), and 10% increase in respiration (n = 66). The magnitude of change in decomposition and respiration was positively related to the magnitude of temperature increase (Figure 5.2), but no significant relationship was observed with the magnitude of temperature increase and primary production, carbon storage, or nitrogen mineralization. The strength of ecosystem process responses to warming varied between habitats (Figure 5.3). The habitat most impacted by warming was the tundra, where warming had significant positive effects on carbon uptake processes (19% increase, n = 35) and efflux processes (30% increase, n = 22). Freshwater habitats were the only other habitat type to show a significant ecosystem process response to warming (Figure 5.3). Unlike in the tundra, only carbon efflux processes increased in freshwater habitats (21% increase, n = 29), while carbon uptake processes had little consistent response to warming.

Addition of nitrogen, and the combination of nitrogen and phosphorus, had a significant effect on primary production (10% and 30% increase, respectively). NP-addition, but not the addition of N alone, had a significant effect on decomposition (11% increase, n = 17). The magnitude of nitrogen addition did not significantly relate to the strength of effect on any of the five ecosystem processes. The combination of warming and nutrient addition had additive effects on decomposition (24% increase, n = 12) and synergistic effects on respiration (43% increase, n = 12).

In contrast, species invasions had little consistent impact for any of the ecosystem processes examined (Figure 5.1). Acidification had strong negative effects on decomposition (40% decrease, n = 18), but no effect on the other ecosystem processes.
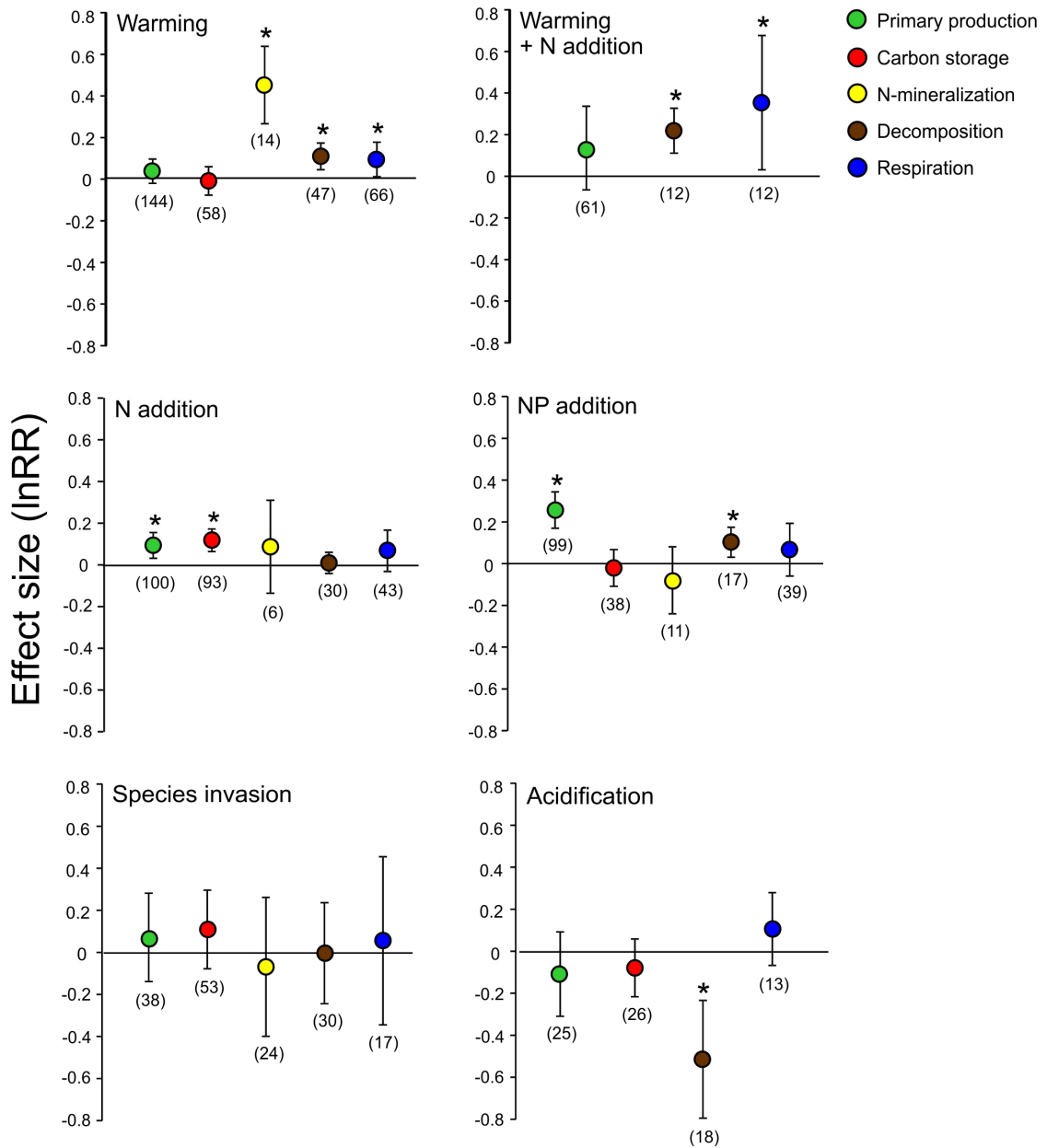
Figure 5.1: Response of five ecosystem processes to six human-induced drivers of environmental change. Shown are the average weighted responses (± 95% CI). Responses that significantly differ from zero, according to the 95% CIs, are indicated with an asterisk. The values in parentheses represent the number of responses included in the analysis.
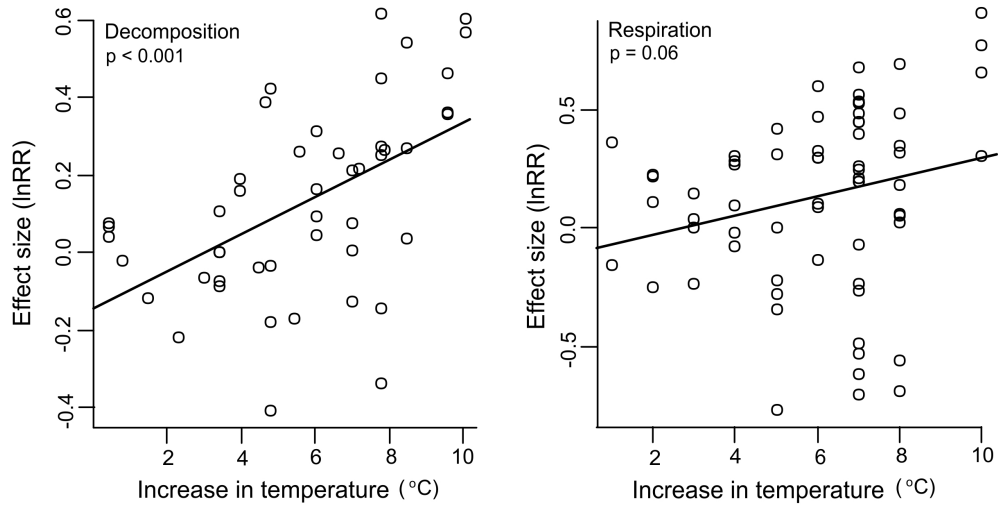
Figure 5.2: Relationship between the magnitude of temperature increase (°C) and the warming response of decomposition and respiration.
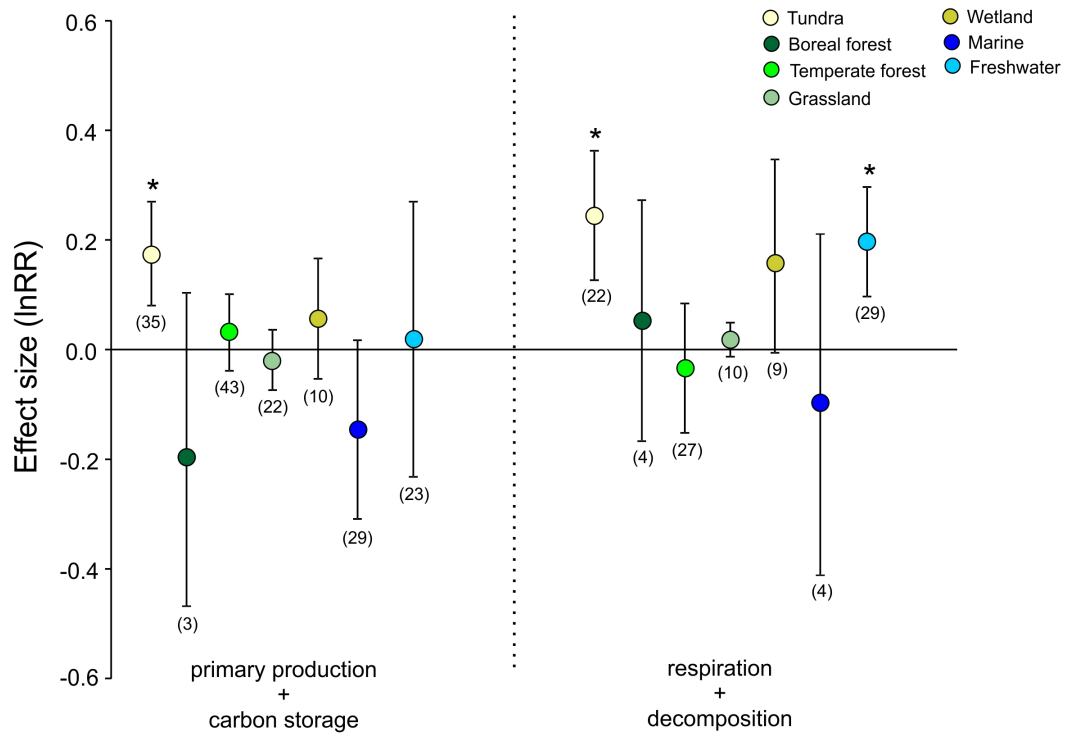
Figure 5.3: Response of ecosystem processes that influence carbon uptake (primary production and carbon storage) and carbon efflux (respiration and decomposition) to warming among 7 aquatic and terrestrial habitats. Shown are the average weighted responses (± 95% CI). Responses that significantly differ from zero, according to the 95% CIs, are indicated with an asterisk. The values in parentheses represent the number of responses included in the analysis.

5.5   Discussion

There is growing concern over the impact of human activity on the functioning of ecosystems. Predicting the impacts of human activity on ecosystems around the world requires an understanding of the general trends in how ecosystem processes respond to human-induced environmental changes. Our results show that, in contrast to the significant negative impact of species invasions on local biodiversity (Murphy & Romanuk 2014), invasions by non-native species do not have consistently strong effects on several ecosystem processes. Instead, warming primarily influenced the ecosystem processes we examined.

The strong effects of warming on several ecosystem processes is consistent with the metabolic theory of ecology, which predicts that the temperature dependence of metabolism is the underlying driver of changes to ecosystem processes such as primary production and respiration (Brown et al. 2004). Across all warming studies we observed significant positive effects of warming on decomposition and respiration, but no consistent effect of warming on primary production and carbon storage. Heterotrophic metabolism is more sensitive to changing temperatures compared to primary producer growth rates (Lopez-Urrutia et al. 2006), and the ability of warming to shift ecosystems to a more heterotrophic dominated state is increasingly demonstrated (O'Connor et al. 2009, Kratina et al. 2012). The shift to a more heterotrophic state implies that ecosystems will result in a positive feedback for further climate warming through decreased primary production and/or increased ecosystem respiration, thus leading to a net release of carbon into the atmosphere (Friedlingstein et al. 2006). That we observed no overall effect of warming on primary production yet strong effects on decomposition (12% increase) and respiration (10% increase) suggests that, in general, warming may lead to a net release of carbon to the atmosphere. In addition, the positive relationship between the strength of decomposition and respiration responses, but not primary production or carbon storage responses, to the intensity of warming implies that higher temperatures further compromise the capacity of ecosystems to store carbon (Yvon-Durocher et al. 2010).

When we examined warming responses between habitats we found that tundra and freshwater ecosystems were the only habitats whose ecosystem processes were significantly influenced by warming. The strong positive responses to warming for processes that store carbon and those that release carbon in the tundra is not surprising given the temperature-limited nature of tundra ecosystems (Salzer et al. 2009). We observed a strong disparity between the effects of warming on processes that store carbon versus processes that release carbon in freshwater ecosystems. No overall effect of warming on primary production and carbon storage combined with a significant 21% increase in decomposition and respiration suggests that freshwater ecosystems are particularly vulnerable to compromised carbon sequestration capacity with climate change.

The significant increase in primary production that we observed with nutrient addition is not surprising given that nitrogen availability constrains plant growth across many terrestrial and aquatic ecosystems (Vitousek & Howarth 1991). Other nutrient addition syntheses have also demonstrated the ability for nitrogen to increase the carbon sink potential of ecosystems (LeBauer & Treseder 2008; Xia & Wan 2008; Lu et al. 2011). Increased N content of plant material will often increase decomposition rates (Vitousek et al. 1997). We observed an additive effect of nutrient addition and warming on decomposition. The combined effect of nutrient addition and warming on respiration was much more pronounced, leading to a synergistic effect where respiration with the two drivers combined was almost double the sum of individual nutrient and warming respiration responses. The synergistic effect of warming and nutrient addition on respiration highlights the need to further study the combined ecosystem impacts of multiple stressors as there is a potential for cumulative effects that might not be predictable when only considering drivers individually (Crain et al. 2008). The potential for synergistic effects of warming and nutrient addition on ecosystem processes is also important to consider given the strong response of nitrogen mineralization to warming (62% increase). Large increases in N-mineralization could mean that ecosystems not especially vulnerable to high anthropogenic nitrogen inputs, for example tundra and boreal forests, will still be affected by amplified responses to warming and nutrients (Hobbie et al. 2002).

The only ecosystem process that was influenced by acidification was decomposition, which was 40% lower in acidified treatments compared to controls. Decreased decomposition in aquatic ecosystems following acidification is well recognized (Lecerf & Chauvet 2008) and is generally attributed to a reduction in the abundance and diversity of acid-sensitive microorganisms that are key to the decomposition process (Clivot et al. 2013). The strong, yet opposite, effects of warming and acidification on decomposition that we observed highlights the need for further studies to consider the interactive effects of warming and acidification on decomposition.

Invasions by non-native species have been associated with increases in primary production, carbon storage, and decomposition (Liao et al. 2008), but we found no consistent effects of species invasions on ecosystem processes. As opposed to the other drivers considered in this meta-analysis, which are all abiotic, species invasions are a biotic driver of change. The impacts of biotic factors on ecosystem processes are harder to decipher due to the complex interactions associated with biotic changes to an ecosystem (Ehrenfeld 2010) and the context-dependent nature of the effects of species invasions on ecosystem processes.

Several recent studies have shown that the overall impact of environmental change on ecosystem functions indirectly depends on the impact of the driver to biodiversity change (Isbell et al. 2013; Hautier et al. 2015). Our results show that the human-induced environmental changes most important in altering several ecosystem processes differs from the environmental changes that most strongly drive local biodiversity loss. Thus, further studies that disentangle the role of direct environmental change effects with effects mediated through biodiversity loss will be crucial in predicting the ecosystem level effects of global change.

5.6   Acknowledgments

CHAPTER 6

CASCADING EFFECTS OF CLIMATE CHANGE ON PLANKTON COMMUNITY STRUCTURE

The work presented in Chapter 6 is currently in review as:

Murphy GEP, Romanuk TN, Worm B. Cascading effects of climate change on plankton community structure. Global Change Biology.

6.1   Abstract

Plankton communities account for at least half of global primary production and play a key role in the global carbon cycle. Climate change and ocean acidification may drive novel ecological interaction chains in these communities from the bottom and top of the food web. Yet, the relative importance of these potentially complex interactions has not yet been quantified. Here we examine the isolated and combined effects of warming, acidification, and declines in phytoplankton and predator abundances in a series of factorial experiments. We find that warming directly impacts both the top and bottom of the food web, but that the intermediate trophic groups are more strongly influenced by indirect effects mediated by altered top-down interactions. Direct manipulations of predator and phytoplankton abundance further support these results and a meta-analysis of published experiments indicates more general top-down effects of warming, with important differences between freshwater and marine plankton communities. Our results reveal that the trophic effect of warming cascading down from the top of the plankton food web is a powerful agent of global change.

6.2 Introduction

Plankton communities play a crucial global role by contributing at least half of global primary production, forming the foundation of aquatic food webs, transferring biomass to higher trophic levels, and influencing the global carbon cycle, (Roemmich & McGowan 1995; Falkowski et al. 1998; Chassot et al. 2010). Although several studies have demonstrated significant impacts of climate change on plankton communities, including, decreased biomass and productivity (Boyce et al. 2010), reduced body size (Garzke et al. 2015; Sommer et al. 2016), and a shift from autotrophic to heterotrophic dominance (O'Connor et al. 2009; Sommer & Lewandowska 2011), the interaction chains by which plankton-based food webs are affected remain poorly understood and difficult to predict. More generally, we know that complex interaction chains are arising from human-driven environmental change, which include both direct and indirect effects (Gilman et al. 2010; Worm & Paine 2016).

While abiotic factors such as elevated temperature and decreased pH can directly affect the physiology and behavior of planktonic organisms (Kroeker et al. 2010; Cripps et al. 2015), changes in predator-prey dynamics can drive cascading trophic effects. Indirect trophic effects of climate change may be as important, or potentially more important, as direct non-trophic effects in shaping aquatic communities (Wernberg et al. 2012; Alsterberg et al. 2013), however, few studies have addressed this for multitrophic plankton communities. Here we use two parallel factorial experiments of warming combined with acidification, and predator removal combined with phytoplankton biomass decline to disentangle the single and combined impacts of global change on plankton community structure, including their indirect effects and cascading interaction chains. Then, we employ a meta-analysis of experimental warming studies to explore the generality of our results across widely different plankton communities, both freshwater and marine

6.3 Methods

6.3.1 Study System

We collected rock pool plankton communities from Prospect, Nova Scotia, Canada (43°29'26"N, 65°43'10"W) in October 2012. Rock pools are common in the supralittoral zone along rocky coasts around the world and are well-established experimental models.

The rock pool communities used in the experiments are populated by a variety of microbes, algae, phytoplankton, zooplankton and small invertebrates. We measured the densities of ten zooplankton species that we classified into functional groups based on five trophic roles. We determined feeding interactions between species from feeding trials and literature review. Two predators occupy the community, a cyclopoid copepod (*Microcyclops varicans*), which is the top predator, and a predatory flatworm (*Gyratrix sp*), which occupies the role of mesopredator. Herbivores are represented by cladocerans (*Alona sp.*), nematodes, and an amphipod (*Gammarus oceanicus*). Omnivores are represented by calanoid copepods (*Acartia sp.*), and an ostracod (*Cyprinidae eucypris*). Detritivores are represented by harpacticoid copepods, an oligochaete (*Limnodrilus hoffmesteri*), and an aquatic springtail (*Archisotoma sp.*).

Once collected, communities were held in aquaria for three weeks and then transferred to 90 1500-ml microcosms. Microcosms were maintained at 21 °C on a 12-hr light/dark cycle. After a two-week acclimation period, the zooplankton communities in several of the microcosms had diverged substantially from the community composition present in the majority of the microcosms. Therefore, we chose 72 microcosms that had similar zooplankton community compositions to use in the experiments, resulting in four replicates for each treatment. The water volume was kept constant throughout the experiments by adding filtered rock-pool water, when necessary.

6.3.2 Experimental Design

We conducted two parallel experiments that each followed a 3 x 3 factorial fully crossed design. In experiment A, we elevated the microcosm water temperature by 0, 4, or 8 °C and reduced the pH by 0, 0.4, or 0.8 pH units. In experiment B, we directly manipulated top predator abundance and phytoplankton density to simulate the negative impact that warming is expected to have on the top and bottom of the food web. The rationale for this control experiment was to analyze the effects of the biotic changes that typically occur with warming, while eliminating the other abiotic influences of warming on the plankton community. Experiment B consisted of three predator removal treatments: no removal, 50% removal, and 100% removal, crossed with three light reduction treatments: 12 hours of light per day, 6 hours of light per day, and 3 hours of light per day.

In experiment A, water temperature was manipulated by placing microcosms on heating pads. Averaged across the eight weeks, the temperature in the control microcosms was 21.54 °C (min. = 20.94 °C, max. = 22.06 °C). The moderate warming treatment increased average temperature by 4 °C to 25.55 °C (min. = 24.81 °C, max. = 26.44 °C), and the severe warming treatment increased average temperature by 7.7 °C to 29.22 °C (min. = 28.11 °C, max. = 29.75 °C). Sulfuric acid (H_2SO_4) was used to reduce the pH of the microcosms. Each week the pH was measured prior to acid additions, and acid was added to reduce the ambient pH by either 0.4 or 0.8 units. Target pH was determined according to the ambient pH of the individual microcosms before the start of the experiment, which ranged from 7.57 to 8.09. The pH was continually monitored and acid was added on a weekly basis, as needed to continually reduce the pH to the prescribed treatment levels. Averaged across the eight weeks, the pH in the control microcosms was 8.08 (min. = 7.97, max. = 8.15). The moderate acidification treatment decreased average pH measured after weekly acid addition by 0.59 to 7.49 (min. = 7.16, max. = 7.67), and the severe acidification treatment decreased average pH measured after acid addition by 0.84 to 7.24 (min. = 7.02, max. = 7.41).

In experiment B, we performed weekly predator removals by examining the entire contents of each microcosm under a stereomicroscope and manually removing 0%, 50%, or 100% of the total number of cyclopoid copepods present. Only adult copepods were removed since juvenile and nauplii stages could not easily be distinguished from other copepod taxa. The removal of cyclopoid copepods resulted in a significant gradient in top predator abundance among the three removal treatments (p < 0.001). Averaged over the course of the experiment, the abundance of cyclopoid copepods in the control treatment (30.04 +- 0.89 SE) was 30% higher than the 50% removal treatment (20.89 +- 1.95 SE, p = 0.005) and 67% higher than the 100% removal treatment (9.83 +- 1.5 SE, p < 0.001). The light reduction treatments resulted in a significant decrease in total phytoplankton concentration (p = 0.04) and a reorganization of the phytoplankton community (p<0.001), with lower concentrations of cyanobacteria and cryptophyte phytoplankton (p<0.001), higher concentration of green algae (p = 0.024), and no change in diatoms (p = 0.493).

Each treatment was replicated four times. Both experiments ran for 8 weeks each. We monitored zooplankton density by performing weekly live counts on two 50-ml sub-samples from each microcosm. After counting the individuals present in the sub-samples, the entire contents of the microcosm were observed under a stereomicroscope to determine whether a species was present in the microcosm but absent in the sub-sample. If this was the case then the species density was recorded as 0.5 to represent its presence at low abundance, in the community. Total chlorophyll-a concentration and the concentration of four algae classes (green algae, diatoms, cryptophyta, and cyanobacteria) was measured weekly from two 25-ml sub-samples using a laboratory spectrofluorometer (bbe-moldaenke, Germany).

Trophic density measurements were averaged across the duration of the experiment, excluding the pre-treatment counts (Figures D.2 and D.3). We conducted two-way multivariate permutation-based analysis of variance (PERMANOVA) to test the single and interactive effects of (1) warming and acidification and (2) predator removal and light reduction on the trophic composition of the zooplankton community for each experiment. Trophic density data were $\log_{10}(x+1)$-transformed to scale down densities of highly abundant trophic groups and increase the importance of less dense trophic groups in the analysis. The PERMANOVA was conducted on a Bray-Curtis similarity matrix. We used zero-adjusted Bray-Curtis similarity matrix for the trophic density data to dampen the fluctuations of the metric for near-blank samples (Clarke and Gorley 2006). Residuals were permutated under a reduced model with 999 permutations. The null hypothesis was rejected when $p < 0.05$.

We conducted factorial two-way ANOVAs to analyze the single and interactive effects of (1) warming and acidification and (2) predator removal and light reduction on the zooplankton and phytoplankton trophic group densities for each experiment. All data were $\log_{10}(x+1)$-transformed prior to analyses to assure homogeneity of variance and normality. The null hypothesis was rejected when $p < 0.05$.

To assess how warming, acidification, predator removal, and light reduction affect the trophic composition of the plankton communities through direct and indirect pathways we utilized structural equation models (SEM). SEMs simultaneously examine direct and indirect pathways between drivers and trophic group densities while

accounting for correlations between multiple response variables (Grace 2006). We analyzed each experiment separately. When constructing the *a priori* models we used a slightly simplified model that included data on the densities of top predators, mesopredators, herbivores, and phytoplankton, since exploratory models suggested that these variables were significantly influenced by the drivers and each other. Pathways between trophic groups were based on known feeding interactions determined through a combination of feeding trials and literature reviews (Figure D.4).

Data were log-transformed to ensure they met the assumptions of multivariate normality. We report standardized path coefficients, which indicate the relative strength and direction of the relationship between variables. The model parameters were estimated using maximum likelihood. When path coefficients were not significantly different from zero ($p > 0.05$) they were removed from the model.

PERMANOVA analyses were conducted using PRIMER (version 7.1) with PERMANOVA+ (version 1.0, Clarke & Warwick 2001). ANOVAs were conducted in R version 3.2.2 (R Development Core Team 2015). SEM analyses were performed using the *lavaan* package in R (Rosseel 2012).

6.3.3 Meta-Analysis

We used a meta-analysis of published warming experiments to determine if our results are generalizable across other marine and freshwater plankton climate change studies. We searched for studies that measured the effect of warming on the density or biomass of predatory zooplankton, herbivorous zooplankton, and phytoplankton. To be included in our analysis, studies had to provide density or biomass measurements for all three trophic groups in both an ambient and experimentally warmed treatment. When measures were reported for multiple sampling dates we averaged values across dates. We evaluated the impact of warming on the trophic group density/biomass across studies in two ways. First, we performed a weighted random effects meta-analysis using the commonly used response ratio [$RR = \ln(\bar{X}_{warmed}/\bar{X}_{ambient})$] as the effect size, to compare the density/biomass of the three trophic groups in the ambient and warmed treatments. A total of 16 studies representing 28 responses to warming for each trophic group were included. In order to quantify the direct and indirect effects of warming on the trophic

groups across studies we used structural equation models to fit the data from each individual study to an *a priori* model and used the standardized path coefficients as effect sizes in a weighted random effects meta-analysis. We obtained 12 datasets to use in the analysis. Models were fit in the *lavaan* package in R (Rosseel 2012). We used chi-square tests to determine how well each dataset fit the *a priori* model and only models that did not significantly differ from the *a priori* model were included in the meta-analysis (n = 10). The results including all models (n = 12) are shown in Figure E.1. In both meta-analyses, effect sizes were weighted according to their sampling variances and the Q-statistic was used to test for effect size heterogeneity. Meta-analyses were conducted in the *metafor* package in R (Viechtbauer 2010).

6.4   Results

6.4.1 Warming X Acidification Experiment

Multivariate PERMANOVA detected a significant effect of warming and acidification on trophic composition of the zooplankton community (warming pseudo-F = 54.86, p = 0.001; acidification pseudo-F = 5.08, p = 0.002). A significant interaction between warming and acidification on the trophic composition of the zooplankton community was detected (pseudo-F = 3.23, p = 0.004).

ANOVA indicated that warming significantly reduced the density of all zooplankton trophic groups (p < 0.001) with the exception of the mesopredator flatworms, which had significantly higher density in the warmed treatments (p = 0.001) (Figure 6.1; Table D.1). We observed an interaction between warming and acidification on detritivore density (p = 0.005), and a marginally insignificant interaction on herbivore density (p = 0.086); yet the direction of the effect was opposite for the two groups. Acidification strengthened the negative effect of warming on herbivore density, while acidification dampened the negative effect of warming on detritivore density (Figure 6.1). Herbivores were the only zooplankton trophic group impacted by acidification alone, with significantly lower herbivore density in the acidification treatments (p = 0.002).

Acidification, but not warming, nor the combination of acidification and warming, influenced total phytoplankton concentration, although we only observed a significant decline in total phytoplankton in the severe acidification treatment (p = 0.049), and not

the moderate acidification treatment (p = 0.746). Warming and acidification had varying effects of the concentration of the four classes of phytoplankton (Table D.1). The absence of a significant effect of warming on total phytoplankton concentration was due to the dichotomous effect of warming on the different phytoplankton classes. Warming significantly increased the concentration of cryptophyta (p = 0.017) and diatoms (p < 0.001), but significantly decreased the concentration of green algae (p = 0.017) and cyanobacteria (p = 0.006).
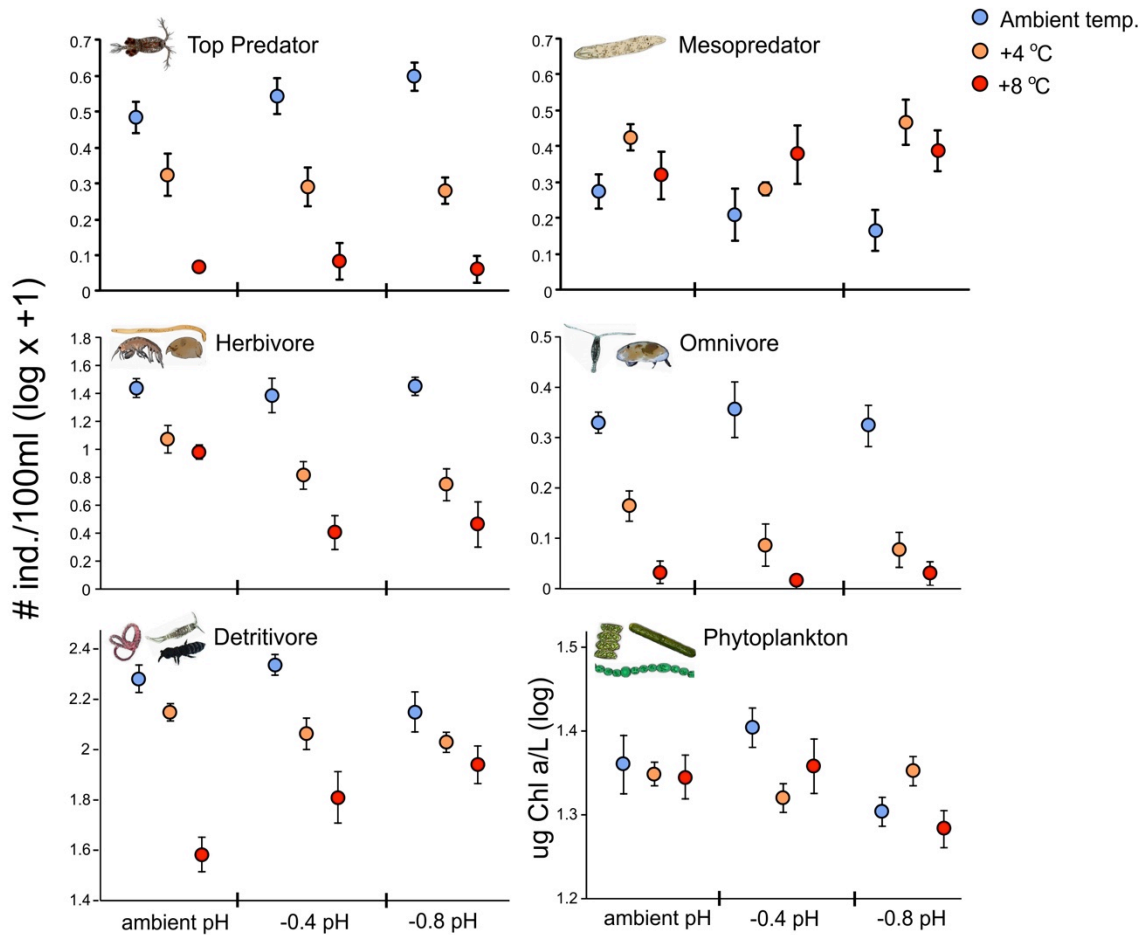
Figure 6.1: Warming experiment. Response of different trophic groups to warming and acidification. Average densities of six trophic groups (mean +/- 1SE, n = 4) are shown for each experimental treatment.

6.4.2 Predator Removal X Light Reduction Experiment

Multivariate PERMANOVA detected a significant effect of top predator removal and light reduction, but not an interaction between the factors, on trophic composition of the zooplankton community (removal pseudo-F = 6.92, p = 0.001; light reduction pseudo-F = 2.76, p = 0.018).

ANOVA indicated that the density of the mesopredator flatworm was significantly higher in the 100% removal treatment (p < 0.001), but not in the 50% removal treatment, compared to no removals (Figure 6.2). Top predator removal also resulted in a marginally insignificant decline in herbivore density (p = 0.087) and a marginally insignificant increase in detritivore density (p = 0.06), while no effect of removal was observed for the abundance of omnivore zooplankton (Table D.2). According to the ANOVA, the cascading effects of top predator removal did not extend to the phytoplankton community, as we observed no significant effects of the removal treatments on total phytoplankton density or the density of any of the phytoplankton taxa (Table D.2). The only zooplankton trophic group significantly impacted by light reduction was the detritivores, where we observed significantly lower density in the 6-hr light treatment compared to the control (p < 0.001). We found no interactive effects of predator removal and light reduction on the densities of any of the zooplankton or phytoplankton trophic groups (Table D.2).
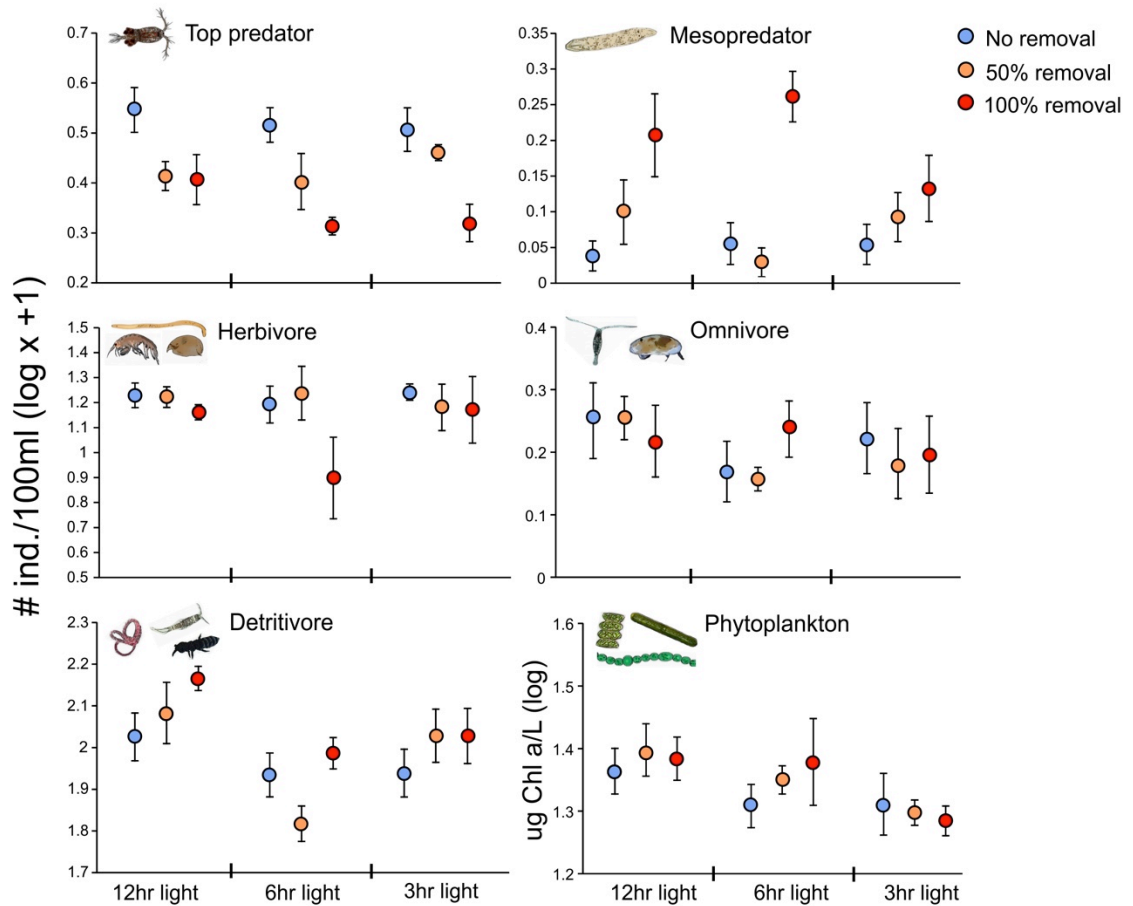
Figure 6.2: Control experiment. Response of different trophic groups to top predator removal and light reduction. Average densities of trophic groups (mean +/- 1SE, n = 4) are shown for each experimental treatment.

6.4.3 Structural Equation Models

Structural equation models indicated strong direct effects of warming on top predators and phytoplankton, but revealed no direct impacts of warming on the two intermediate trophic groups (Figure 6.3a). Instead the decline in herbivore density from warming that was reported in the ANOVA analyses occurred through indirect effects of cascading trophic interactions (standardized path coefficient = -0.27). These indirect effects were just as strong as the direct effect of acidification on herbivore density (standardized path coefficient = -0.27). The structural equation models for both experiments revealed strong top-down trophic cascades (Figure 6.3). While removing predators directly resulted in a cascade that extended from the top predator to the phytoplankton (Figure 6.3b),

experimental warming had a strong direct effect on top predator density (standardized path coefficient = -0.94) that led to a trophic cascade through indirect impacts on the mesopredators and herbivores, but unlike direct predator removal, did not extend to the phytoplankton (Figure 6.3b). Instead, the SEM results suggest that the decline in phytoplankton we observed in this experiment was predominantly due to the direct effects of warming (standardized path coefficient = -0.41) and acidification (standardized path coefficient = -0.37), rather than cascading trophic interactions. The models for both experiments revealed no significant bottom-up effects from declining phytoplankton on consumer trophic group densities (Figure 6.3).
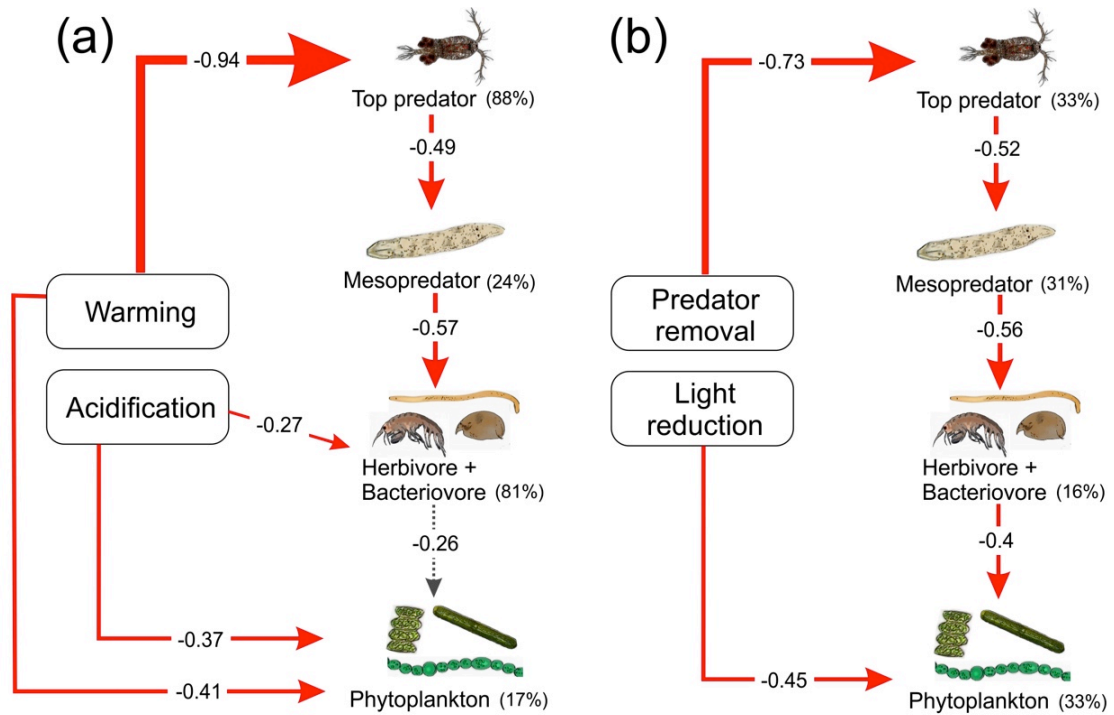
Figure 6.3: Direct and indirect effects of climate change. Path diagrams showing how (a) warming and acidification and (b) top predator removal and light reduction are associated with changing consumer and producer densities. Results are from a fitted structural equation model. Standardized path coefficients are shown next to each path and indicate the relative strength of the relationship between variables. Solid paths are statistically different from 0 at $p < 0.05$ and line thickness is proportional to the relative weight of the standardized path coefficient. Red lines represent significant negative relationships, blue lines represent significant positive relationships, and dotted lines represent non-significant effects. Percentages represent the explained variance. All densities were log-transformed prior to analysis. The omnivore and detritivore taxa did not significantly contribute to the trophic cascade and were therefore not included in the model to avoid over-fitting.

6.4.4 Meta-Analysis

Across all studies, warming significantly reduced predatory zooplankton by 23% and herbivorous zooplankton by 39%, but did not significantly impact phytoplankton concentration (Figure 6.4a). A Q-test revealed significant heterogeneity that was reduced by splitting studies into marine and freshwater. This revealed that warming had a significant negative effect on the concentration of marine phytoplankton (Figure 6.4b) and a positive, yet not significant, effect on the concentration of freshwater phytoplankton (Figure 6.4c). In contrast, warming had little effect on marine zooplankton and a significant, negative effect on both trophic levels of freshwater zooplankton (Figures 6.4b and 6.4c). The meta-analysis of structural equation models from 10 warming studies with sufficiently detailed data corresponded with these findings, indicating a significant direct effect of warming on phytoplankton in marine ecosystems and a significant direct effect of warming on predatory zooplankton in freshwater ecosystems, but not vice versa (Figures 6.4e and 6.4f). While warming influenced the top and bottom trophic groups in marine and freshwater ecosystems differently, the direct effect of warming on herbivorous zooplankton was comparable. Similar to our experimental results, this effect was weak, not significant, and negative. As in our experiments, the meta-analysis SEM also revealed weak herbivore-phytoplankton interactions across all studies (Figure 6.4d) and in both marine and freshwater communities (Figures 6.4e and 6.4f). We also found a stronger predator-herbivore interaction in freshwater compared to marine plankton communities (Figure 6.4e and 6.4f).
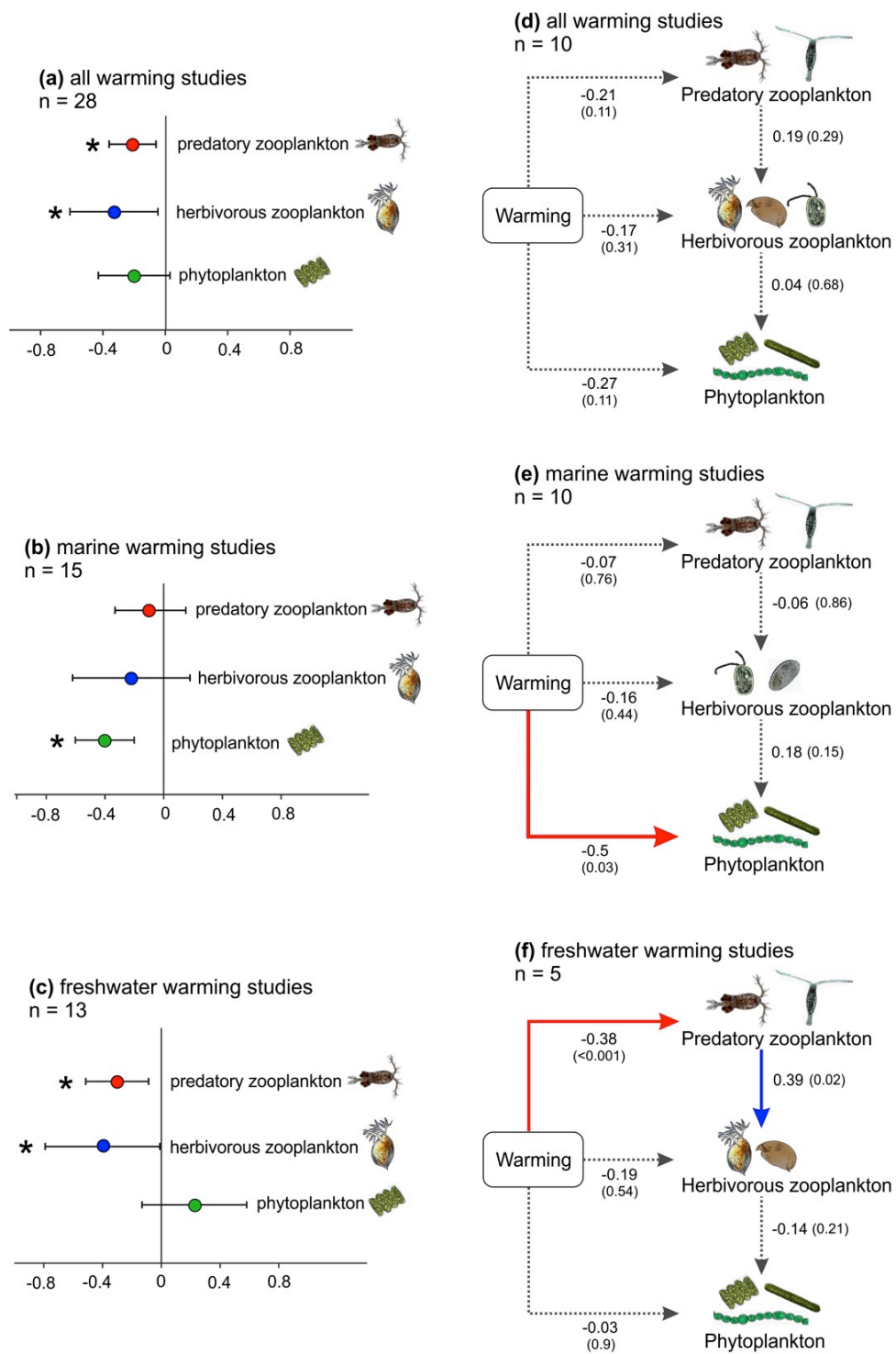
Figure 6.4: Meta-analysis of published warming experiments. Shown are response ratios (a, b, c) and SEM path coefficients (d, e, f). Results are displayed for all studies combined or separated by marine and freshwater studies. Path coefficients indicate the strength and direction of the relationship between variables, and are shown above arrows with the corresponding p-values displayed in brackets. Bold arrows indicate significant negative (red) and positive (blue) relationships (p < 0.05) and dashed arrows indicate non-significant relationships.

6.5 Discussion

Our experiments reveal that elevated temperatures primarily impact the top and bottom of the plankton food web, and suggest that intermediate trophic groups are strongly influenced by altered trophic interactions as opposed to direct effects of changing environmental conditions. Higher trophic levels are generally more susceptible to elevated temperature, as the metabolic demands of consumers are more sensitive to warming than those of primary producers (Lopez-Urrutia et al. 2006). This leads to higher grazing rates and eventually decreased consumer fitness when energy intake by consumers cannot keep up with their metabolic demands (Rall et al. 2010). Strengthened top-down control in plankton communities has been demonstrated in other warming experiments (O'Connor et al. 2009; Sommer & Lewandowska 2011; Kratina et al. 2012) and the strong top-down effects we observed with both direct predator removal and warming emphasizes that warming-induced loss of top-predators can cascade to lower trophic levels.

Structural equation models further supported strong direct effects of warming on top predators and phytoplankton, but revealed no direct impacts of warming on the two intermediate trophic groups. Instead, the changes in density of mesopredators and herbivores that we observed in our experiments appear to be driven by altered predator-prey dynamics. In the absence of the abiotic stresses of warming and acidification, experimental reduction of predators and phytoplankton led to markedly similar path coefficients, providing further evidence that trophic interactions mediated by top-predator declines are the dominant factor controlling intermediate trophic groups. Warming has been shown to alter interactions between trophic groups (Van der Putten et al. 2010; Yvon-Durocher et al. 2010; O'Connor et al. 2009) and increase the strength of indirect trophic interactions (Barton & Schmitz 2009; Marquis et al. 2014). Intermediate trophic groups are particularly vulnerable to altered species interactions through both direct consumption from predators and non-consumptive interactions, such as the effects of predation risk, which are reported to enhance with warming (Miller et al. 2014). Predation risk exerts a strong influence on intermediate trophic groups by increasing metabolic rates and stress hormones, and these effects can be just as strong as those produced by direct consumption (Hawlena & Schmitz 2010). That we found a negligible

direct effect of warming on the two intermediate trophic groups in our experiments, and instead observed strong negative interactions between the prey species and their predators, demonstrates the importance of considering how trophic interactions may be altered with climate change.

Altered trophic interactions led to a major shift in our experimental plankton communities, which was partially driven by a significant increase in mesopredator density with warming and predator removal. Mesopredator release has been described across a range of aquatic and terrestrial ecosystems (Baum & Worm 2009; Ripple et al. 2014). That we observed this phenomenon with both warming and direct predator removal strongly supports the importance of cascading trophic effects. We found that the combined stress of warming and acidification on plankton communities led to differential vulnerability among trophic groups. Some trophic groups were resistant to the interactive effects of warming and acidification, particularly predatory and omnivorous zooplankton, while lower trophic level zooplankton, particularly herbivores and detritivores, were more vulnerable. Furthermore, acidification strengthened the negative effect of warming on herbivore density, while dampening the negative effect of warming on detritivore density. These results show that the combined stresses associated with climate change have the ability to amplify or dampen the singular effects, and this is partly dependent on trophic role.

The interaction strengths from our two experiments were mostly similar; however, a difference in the strength of the herbivore-phytoplankton interaction suggests that warming and acidification weaken herbivore control on phytoplankton. Direct predator and phytoplankton removal led to a strong negative herbivore-phytoplankton interaction, but with warming and acidification this interaction was weaker and not significant. Our results also show that acidification directly impacted herbivorous zooplankton density through increased mortality. A physiological impact of either warming or acidification on grazing ability of zooplankton or a reduction in phytoplankton edibility may be driving a weakened herbivore-phytoplankton interaction. While our study was not designed to quantify zooplankton grazing rates or phytoplankton nutritional content, previous studies have noted little impact of acidification on grazing rates, and instead point to decreased

algal nutritional quality as the driving force behind altered herbivore-producer interactions (Poore et al. 2013; Duarte et al. 2016).

Altered phytoplankton taxonomic composition can also play a role in changing the strength of zooplankton-phytoplankton interactions. Warming and acidification resulted in a shift from less edible (cyanobacteria) to more edible (diatoms) phytoplankton taxa in our experimental communities. The absence of a strong trophic interaction between zooplankton and phytoplankton with this switch from inedible to edible taxa suggests that warming and acidification may have affected the edibility of diatoms. Numerous studies have reported a decrease in the size of marine phytoplankton with increasing temperature (Sommer et al. 2016). With phytoplankton size being an important factor in determining trophic connections (Boyce et al. 2015), it is possible that warming reduced interaction strength between zooplankton and phytoplankton by selecting for small cell sizes that are less efficiently grazed by zooplankton.

Our meta-analysis largely confirms our experimental results across a wide range of communities and provides more general evidence that warming will exert a stronger direct influence on the top and bottom of food webs, while intermediate trophic groups will be more impacted by changing trophic interactions. Our meta-analysis results also highlight important differences between marine and freshwater plankton studies. We detected a stronger predator-herbivore interaction in freshwater compared to marine plankton communities. Contrary to what would be expected for a predator-prey relationship, this interaction was positive. This disparity may be explained by a difference in the zooplankton taxa reported. All freshwater studies (except our own) reported the abundances of copepods and cladocerans, while marine studies reported the abundances of copepods and microzooplankton (ciliates and HNF). The copepods reported in the freshwater studies are omnivorous and occupy a higher trophic level than the cladocerans; however, it is possible that there was not a strong predator-prey relationship between the two. Interactions between copepods and cladocerans with other species that were present in the experimental communities, but whose abundances were not reported, may have resulted in facilitative interactions, via the copepods improving cladoceran resource availability by preying on competing herbivorous zooplankton. In contrast, microzooplankton comprise a large portion of the copepod diet in the marine

experiments, which resulted in the negative, albeit weak, predator-herbivore interaction in marine studies.

In conclusion, our experiments and meta-analyses show that warming has direct impacts on the top and bottom of plankton food webs, yet top-down effects were stronger in shaping the plankton community through cascading interactions. Our results reveal distinct differences in how trophic groups respond to climate change stressors and provide evidence that intermediate trophic groups are more impacted by cascading trophic interactions than by the direct effects of warming and acidification. We show that alterations in interaction chains from the indirect effects of warming, acidification, and predator decline, can be equally important as direct effects in restructuring plankton communities under climate change. Accurately forecasting the effects of climate change is not possible without understanding its effects on trophic interactions. We emphasize the need for multi-trophic studies of natural plankton communities that partition the net effects of climate change stressors into direct and indirect effects to fully understand the consequences that present and future global change will have on aquatic ecosystems.

6.6 Acknowledgements

CHAPTER 7

CONCLUSIONS

The overall goals of this thesis were to characterize and compare the biodiversity and ecosystem responses to human-induced environmental changes. This included evaluating general trends in responses across drivers, habitats, biomes, and trophic groups, and examining the mechanisms by which global change drivers restructure communities. Here, I summarize my findings and discuss their overall significance as well as future research directions.

7.1 Thesis Summary And Contributions To Knowledge

In chapter 2, I conducted the first globally distributed quantitative evaluation of local biodiversity responses to several human-induced environmental changes that are identified as major drivers of global biodiversity loss. My results showed widespread decline in local species richness by an average 18%, and revealed several trends in biodiversity change among drivers, habitats, biomes, and trophic groups. The largest species loss occurred from land-use change, particularly in the tropics, and due to species invasions, particularly in boreal and northern temperate forests. Furthermore, I found a general trend towards greater species loss in terrestrial habitats compared to aquatic, and for endothermic species compared to ectotherms and producers.

The observed large decreases in local species richness across a wide range of drivers and habitats is significant given the emerging debate in ecology as to whether average trends in local biodiversity are increasing, decreasing, or remaining constant (Gonzalez et al. 2016). My results contrast other recently published data syntheses that have reported

no net loss of local species richness across the globe (Vellend et al. 2013; Dornelas et al. 2014; Supp & Ernest 2014). The results from these former studies have received criticism for not fully accounting for biodiversity change in all types of human exploited habitats and for using time-series rather than spatial references (Cardinale 2014; Gonzalez et al. 2016). I measured species richness change against a common baseline (i.e. impacted sites vs. non-impacted reference sites) and focused on the biodiversity responses to human-driven environmental changes as opposed to a combination of human-impacted and pristine habitats. My analyses clearly demonstrate that most forms of anthropogenic global change have marked negative effects on local biodiversity.

The dataset I compiled in Chapter 2 to quantify trends in local biodiversity change has several geographic biases that made it difficult to robustly compare responses across regions and biomes. Likewise, the authors from other recently published biodiversity change syntheses (Vellend et al. 2013; Dornelas et al. 2014; Gerstner et al. 2014; Supp & Ernest 2014; Newbold et al. 2015) all make mention of similarly extensive geographic biases in their datasets. These geographic data gaps demonstrate that the data used in current biodiversity syntheses does not depict a globally representative sample of local biodiversity change patterns (Gonzalez et al. 2016). Geographic biases hinder the ability to detect and accurately make predictions about how biodiversity is changing on a global scale, and what the consequences of that change are.

In Chapter 3, I determined where the most critical geographic biases in human-driven biodiversity change studies exist across terrestrial biomes based on future levels of threat and impacts of drivers on biodiversity. I showed that inferences about how local biodiversity is changing around the globe will be especially improved by collecting more data on the biodiversity responses to land-use change in tropical and temperate coniferous forests, species invasions and nutrient addition in the boreal forest, and warming in the boreal forest and tropics. Collaborative experimental networks are emerging in ecological research as a powerful method to detect and quantify general ecosystem trends (Borer et al. 2014). To make the most useful predictions of global change, these networks will need to consider the geographic data gaps that currently exist in the ecological literature and capture data that eliminates these biases. By highlighting the biomes where further empirical data is required specific to various drivers, my results

from Chapter 3 will be useful in the design of future global change studies. Given the findings of Chapter 3, future studies should ensure that their data allows for robust comparisons of biodiversity responses to human activities across geographic regions and biomes.

My conclusion from Chapter 2—that local species richness is generally lower in human-dominated habitats—takes into account how environmental changes affect average biodiversity, but does not consider the consistency of community responses to global change. Thus, in Chapter 4, I sought to determine if certain drivers led to more consistent community change, and if habitats and trophic roles influenced the consistency of the response. Generalizable patterns in the variability of responses among replicates can provide insight into the consistency of community change and inform how predictable the responses to global change drivers are (Avolio et al. 2015). This is assessed by analyzing whether replicates within a treatment have similar or varying responses (Fraterrigo & Rusak 2008; Avolio et al. 2015).

My results revealed strong, yet opposite, trends in biodiversity response predictability for species invasions, species removals, and nutrient addition. I showed that the biodiversity decline that is observed following invasions is highly consistent, but only if invasions occur in aquatic habitats and when the invader is a producer. Alternatively, direct species removals led to highly inconsistent biodiversity responses, but only in terrestrial habitats and, as with invasions, only when the removed species was a producer. Nutrient addition led to highly inconsistent abundance responses, but only in aquatic habitats. These results suggest that the accuracy in forecasting community change based on empirically derived estimates will depend on drivers, habitats, and trophic groups. For example, predicting the biodiversity responses of invaders at low trophic levels in aquatic ecosystems may yield more accurate predictions given their highly consistent responses as opposed to the response to invaders at high trophic levels in terrestrial ecosystems.

My analysis of the response predictability to global change drivers also suggests potential differences in how communities restructure after biotic changes (Chase 2007, Myers & Harms 2011; Chase & Myers 2011). That I found invasions more likely to lead to greater community similarity among replicates suggests that deterministic processes might play a stronger role in restructuring communities following invasions. On the other

hand, species removals resulted in greater community divergence, perhaps suggesting a stronger influence of stochastic processes in restructuring communities following removals.

In Chapter 5, I sought to determine the general ecosystem process responses to some of the global change drivers that I examined in Chapter 2. My results show that, in contrast to the significant negative impact of species invasions on local biodiversity (Chapter 2), invasions by non-native species do not have large effects on the average trends of several ecosystem processes. Instead, ecosystem processes were primarily influenced by warming and nutrient addition.

In Chapter 6, I conducted a case study using a multi-trophic aquatic model ecosystem to explore the direct and indirect effects of two prominent global change drivers (warming and acidification). Community responses to human impacts are largely driven by alterations to the structure and dynamics of species interaction networks. Thus, predicting responses to global change is complicated by the potential for cascading species interactions resulting in indirect effects that may either counteract or strengthen the direct effects of global change drivers (Wernberg et al. 2013; Alsterberg et al. 2013; Worm & Paine 2016). My results demonstrated that the nature of warming effects on the plankton community were dependent on trophic role. Top predators and primary producers were primarily impacted by direct effects of warming, while intermediate trophic groups were more strongly impacted by indirect effects mediated by cascading top-down trophic interactions.

The strong top-down effects I observed in my experiments are consistent with other warming experiments and highlight that warming-induced loss of top-predators can cascade to lower trophic levels and completely restructure communities (O'Connor et al. 2009; Sommer & Lewandowska 2011; Kratina et al. 2012). These results provide an appreciation for how altered species interactions from global change drivers can lead to indirect effects that can be equally important as direct effects in restructuring communities. This chapter emphasizes that to fully understand and predict the community-level consequences of human-driven environmental changes it will be necessary to consider both their direct and indirect effects.

7.2   Future Directions

My thesis has highlighted several future research directions that will be important in strengthening assessments of ecosystem and community trends in response to human-driven environmental changes. Most importantly, my research emphasizes the need for more comprehensive and globally representative data on community-level responses to global change drivers. Generalizations of ecosystem consequences to human activities are limited by the quantity and quality of available data.

Published studies of community responses to global change primarily report species richness data, and lack information on community composition and species interactions. Consequently, species richness is the biodiversity metric used in this (Chapters 2, 3, and 4) and many other biodiversity change syntheses (Vellend et al. 2013; Gerstner et al. 2014; Gruner et al. 2016). Species richness provides an important measure of ecosystem performance in regards to stability and maintenance of functions (Hooper et al. 2005; Isbell et al. 2011). However, the popularity of this metric in biodiversity change syntheses is largely driven by its wide usage in the global change literature, rather than its ability to comprehensively describe community change. Species richness alone does not account for compositional and functional shifts in ecological assemblages that can occur with global change (Mendenhall et al. 2012). For example, in Chapter 6 I found no significant change in species richness with warming or acidification, yet the community structure and strength of biotic interactions was highly influenced by both drivers. Several studies have revealed similar outcomes (Mendenhall et al. 2011; Dornelas et al. 2014; Elo et al. 2016). Thus, the need for empirically derived global change data that quantifies impacts to community composition and interaction networks is becoming increasingly recognized (McGill et al. 2015; Worm & Paine 2016).

Another underrepresented element of empirical global change studies is the inclusion of multiple drivers to assess their single and interactive effects. Global change drivers rarely occur independently, and interactions between drivers can amplify or dampen responses (Chapter 6). Thus, more studies that examine the community-level effects of combined drivers are necessary. There is currently not sufficient data in the published literature to robustly synthesize the interactive effects of anthropogenic drivers on local biodiversity.

Efforts to collect comprehensive community response data will allow for the exploration of complex issues regarding the local-scale impacts of human-driven environmental changes. One such issue is how local estimates of biodiversity change translate to regional and global scales (Keil et al. 2011). My thesis focused on local-scale community responses to human impacts. I chose this scale of observation as variation in local species richness more directly influences ecosystem functioning as compared to larger scale changes (Pasari et al. 2013). In addition, the majority of empirical global change data is collected at local scales. However, quantifying biodiversity responses at larger scales may be more relevant for some conservation goals. Further insight into the strength of biodiversity responses to human impacts across scales is crucial for ecosystem management and for addressing global conservation priorities that require a broad-scale approach to understanding biodiversity change (Tittensor et al. 2014).

The non-additive nature of species richness, and scale-dependence of many biodiversity metrics, complicates the translation of local biodiversity change to larger scales (Gotelli & Colwell 2001; Azaele et al. 2015). Use of metrics in future biodiversity change syntheses that are determined by both the spatial distribution and abundances of species (ex. species accumulation curves) may provide a way of generalizing biodiversity trends regardless of scale (Chase & Knight 2013). Of course, the ability to conduct analyses with scale-independent biodiversity metrics requires knowledge of community composition responses to anthropogenic drivers across multiple spatial scales. Currently very little published data fits this description, further demonstrating the need for more comprehensive collection of biodiversity and global change data to uncover generalities in how ecological assemblages respond to particular drivers of change.

Resolving the ecosystem consequences of human impacts also requires a clearer understanding of how direct and indirect effects combine to influence responses. My experimental work emphasized the importance of disentangling the influence of direct abiotic effects and indirect effects via species interactions to better understand how global change drivers alter community structure (Chapter 6). However, my syntheses only examined net effects of drivers on biodiversity and ecosystem processes (Chapters 2 and 5). Recent studies have shown that the overall impact of global change drivers on ecosystem functioning indirectly depends on the extent to which the driver alters

biodiversity (Isbell et al. 2013; Hautier et al. 2015; Trzcinski et al. 2016). Furthermore, the effects of local species loss and many human-induced environmental changes on ecosystem processes have been shown to be comparable in magnitude (Hooper et al. 2012). Yet, the relative importance of direct driver effects, and indirect effects mediated through species loss resulting from the driver, on the functioning of ecosystems across different drivers, ecosystem processes, habitats, and geographic regions has not been examined. This knowledge will yield greater predictive power of the ecosystem responses to global change than the net effects alone.

Finally, my experiments revealed strong impacts of warming and acidification on plankton community structure. Negative effects of climate change on plankton are increasingly recognized. However, the single and combined consequences of climate change stressors on plankton assemblages and the functions they provide are still poorly understood. Plankton communities play a critical global role by influencing the Earth's carbon cycle and forming the foundation of aquatic food webs (Roemmich & McGowan 1995; Falkowski et al. 1998; Chassot et al. 2010). Thus, additional multi-trophic approaches that help elucidate the direct and indirect effects of climate change on plankton communities in different regions and habitats are necessary to better understand the consequences of climate change in aquatic ecosystems.

7.3   Overall Conclusions

My thesis represents the most comprehensive quantitative synthesis to date of anthropogenic global change effects on the magnitude and consistency of biodiversity and ecosystem process responses. A significant challenge in contemporary ecology is improving the predictive power of experimental and observational studies that measure the community and ecosystem level effects of global change drivers. A predictive understanding of how human activities impact ecosystems relies on the ability to identify general trends in community responses. By utilizing the large number of empirical global change data in the published literature, my thesis has illustrated several general trends of local biodiversity and ecosystem process responses across drivers, habitats, biomes, and trophic groups. Furthermore, by quantifying the magnitude of local biodiversity change from numerous anthropogenic drivers, my results will aid future predictive analyses of

how global change will impact the ecosystem services that human well being depend on. In addition, my thesis emphasizes the importance of simultaneously addressing direct abiotic effects and indirect trophic effects in global change research to yield further insight into the community level consequences of human-driven environmental changes.

APPENDIX A

Supplementary material for Chapter 2: Local biodiversity loss from human-induced environmental changes
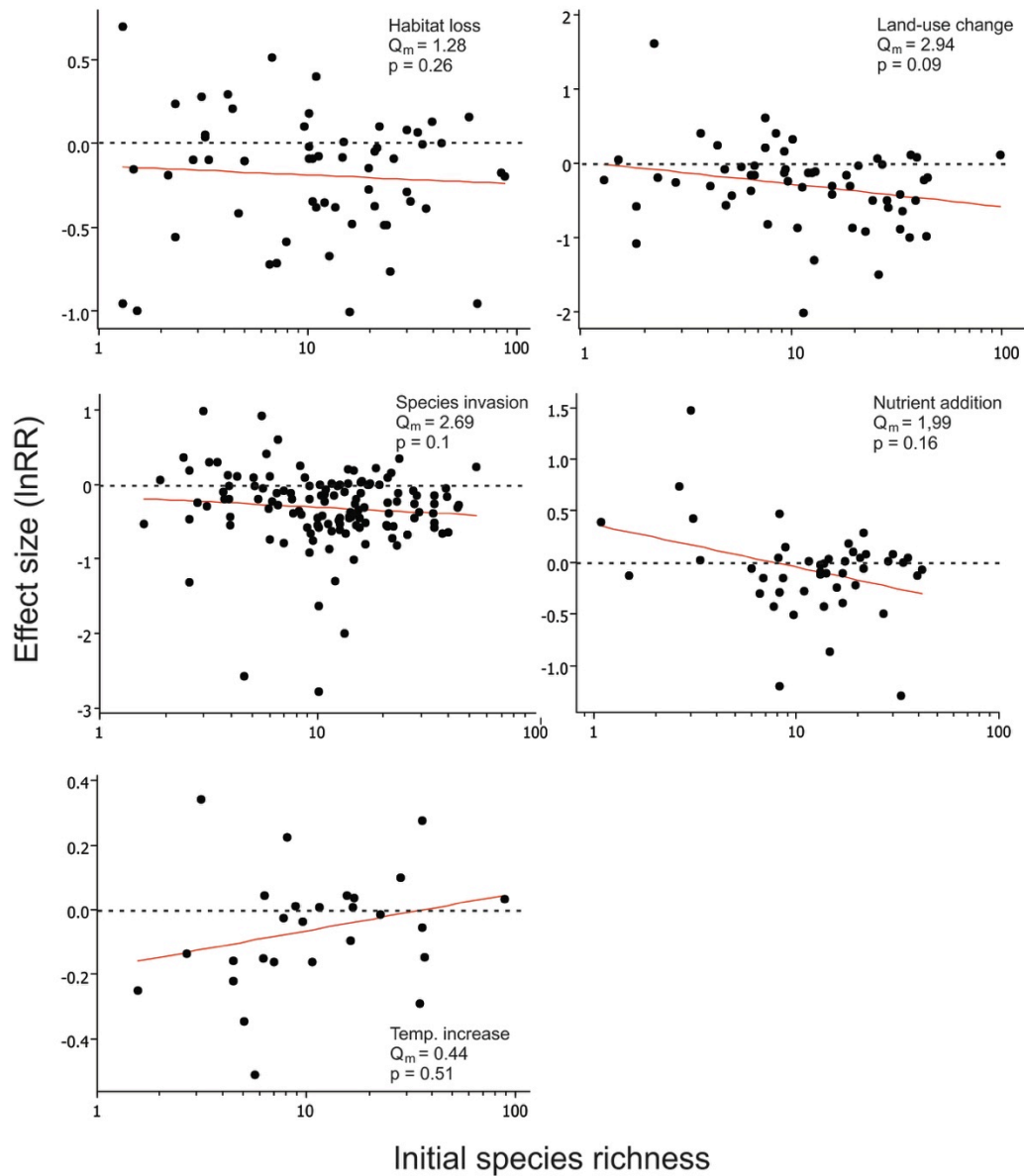
Figure A.1: Relationship between initial species richness and change in species richness for five global change drivers. Habitat loss (A), land-use change (B), species invasion (C), nutrient addition (D), and temperature increase (E).
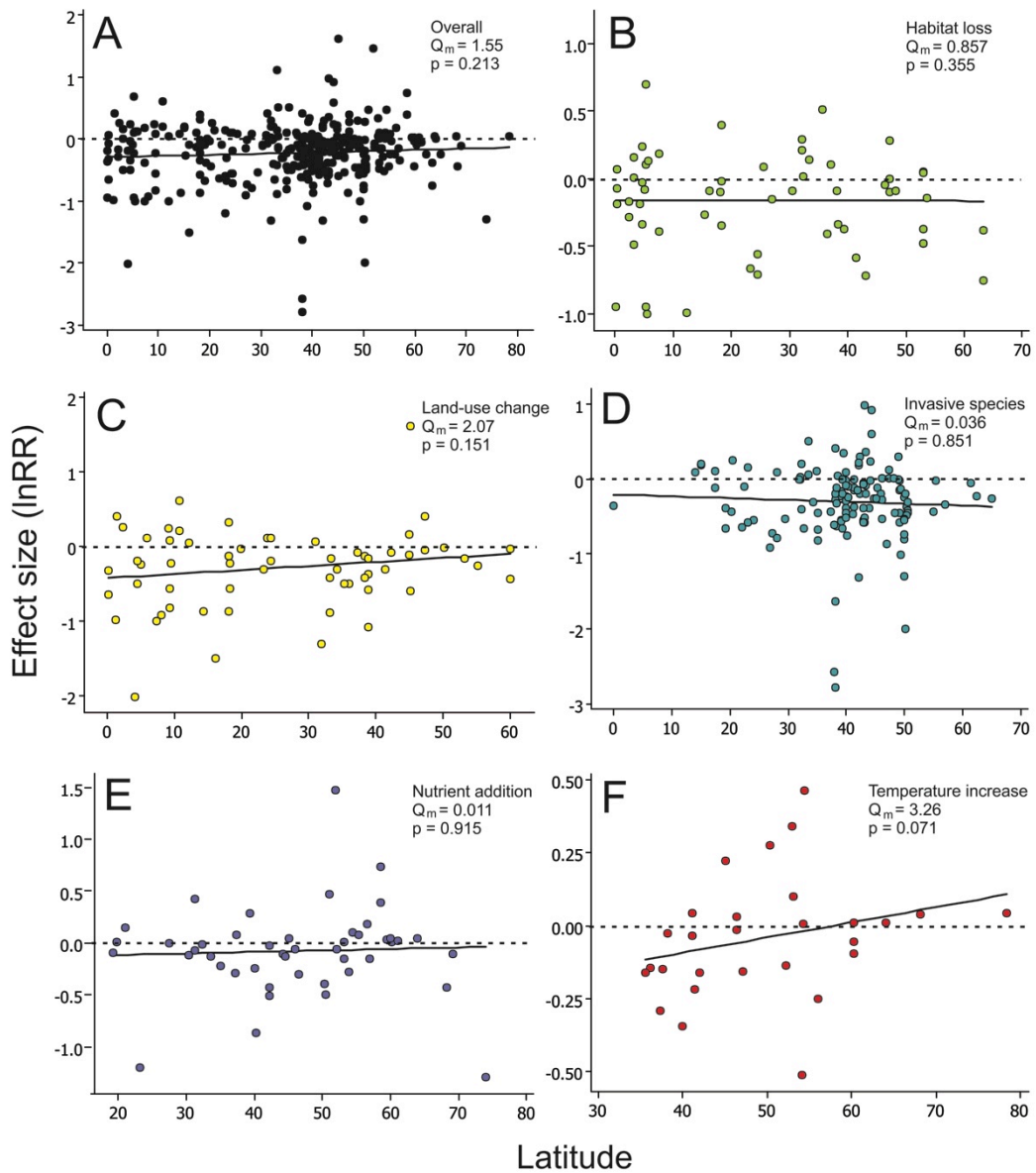
Figure A.2: Relationship between latitude and change in species richness for five global change drivers. All drivers (A), habitat loss (B), land-use change (C), invasive species (D), nutrient addition (E), temperature increase (F).
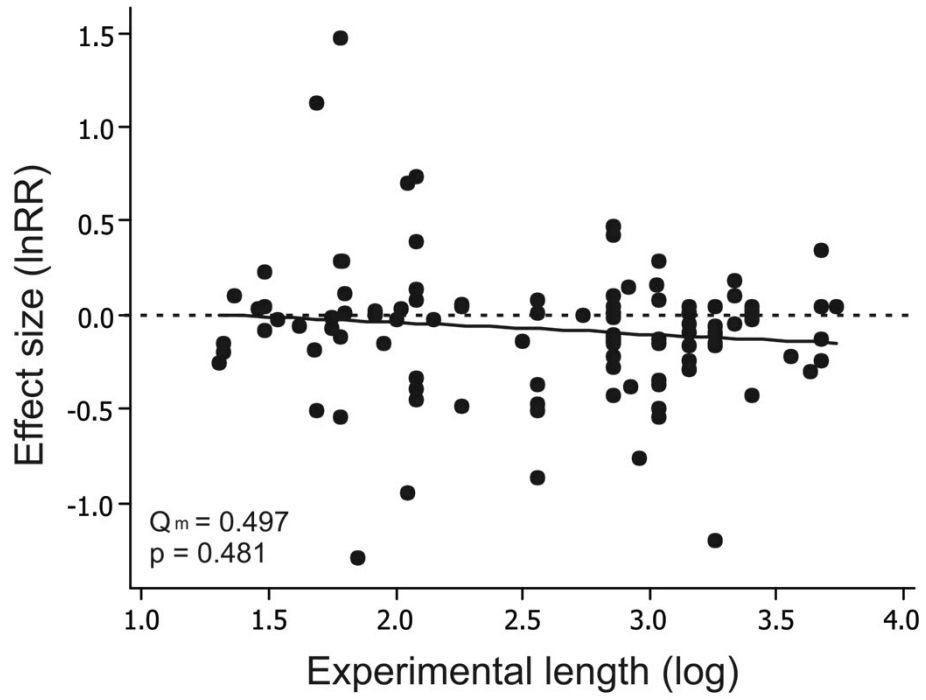
Figure A.3: Relationship between experimental length (days) and response of species richness to global change drivers.

Table A.1: Heterogeneity statistics and corresponding p-values for each of the categorical and continuous factors included the meta-analysis.

Categorical factors		Q_t	p	Q_b	p	Q_w	p
	Disturbance type	219.10	1.00	9.12	0.058	209.98	1.00
	Study type	249.48	0.002	6.83	0.078	242.66	0.004
	Trophic category	209.52	1.00	10.59	0.005	198.92	1.00
	Trophic x Disturbance	214.82	1.00	25.91	0.011	188.90	1.00
	Biome type	157.40	0.99	6.99	0.072	150.39	0.99
	Biome x Disturbance	162.32	0.99	12.88	0.302	149.45	0.99

Initial SR (continuous)		Q_t	p	Q_m	p	Q_e	p
	All disturbances	200.59	1.0	4.61	0.032	195.98	1.00
	Habitat loss	71.07	0.099	1.282	0.257	69.79	0.102
	Land-use change	77.10	0.039	2.94	0.086	74.16	0.053
	Species invasion	158.23	0.041	2.69	0.101	155.54	0.049
	Nutrient addition	16.72	0.99	1.99	0.159	14.72	0.999
	Temp. increase	26.29	0.447	0.441	0.506	25.85	0.416

Latitude (continuous)		Q_t	p	Q_m	p	Q_e	p
	All disturbances	277.06	0.98	1.55	0.21	275.51	0.98
	Habitat loss	69.59	0.14	0.86	0.35	68.74	0.14
	Land-use change	91.93	0.006	2.06	0.15	89.86	0.008
	Species invasion	153.11	0.09	0.036	0.85	153.12	0.08
	Nutrient addition	39.21	0.71	0.01	0.92	39.2	0.68
	Temp. increase	29.15	0.35	3.26	0.07	25.89	0.47

Exp. length (continuous)		Q_t	p	Q_m	p	Q_e	p
	All disturbances	36.69	1.00	0.497	0.481	36.19	1.00

APPENDIX B

Supplementary material for Chapter 3: Data gaps in local biodiversity change studies across the Earth's biomes
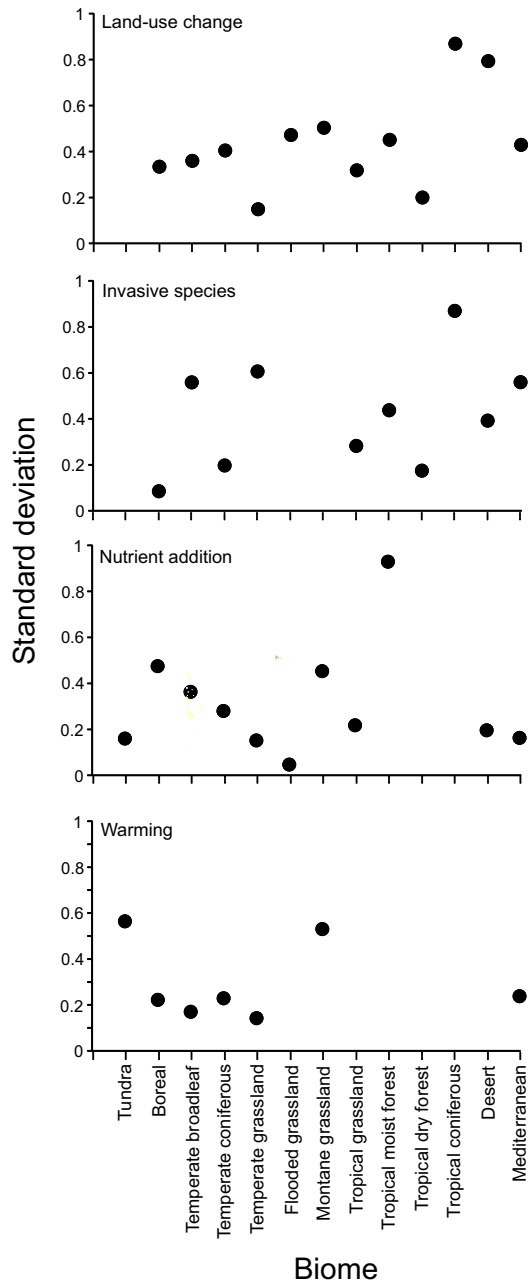
Figure B.1: Variance (given as standard deviation) in the magnitude of change in species richness following four human drivers of change.

APPENDIX C

Supplementary material for Chapter 4: Predictability of community responses to human-induced environmental changes
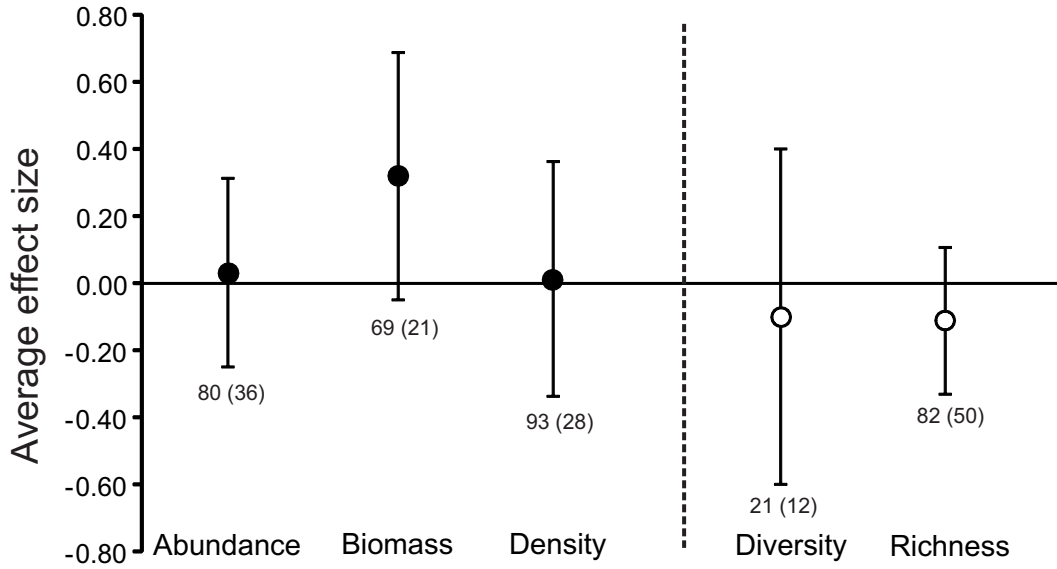
Figure C.1: Average response ratios and 95% confidence intervals for abundance and diversity response predictability between different measures of abundance or diversity. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken.
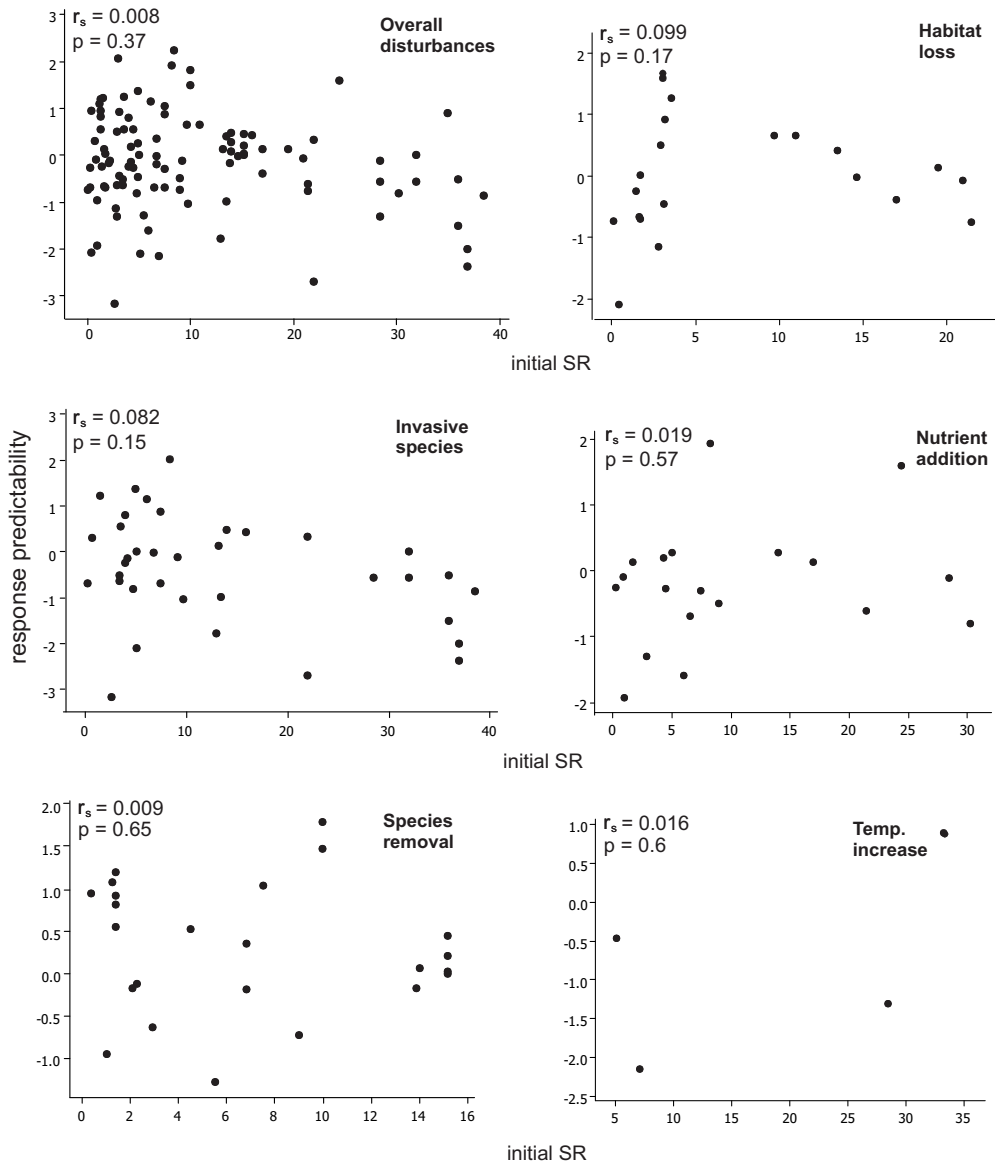
Figure C.2: Relationship between initial species richness (SR) and the response ratio for diversity response predictability for different global change drivers. Shown are the Pearson correlation coefficients and the corresponding p-values.

APPENDIX D

Supplementary material for Chapter 6: Cascading effects of climate change on plankton community structure

Table D.1: Results of two-way ANOVA testing the effects of warming, acidification, and their interaction on the average densities of zooplankton and phytoplankton groups. All densities were log $(x+1)$ transformed for the analyses. Significant effects ($p < 0.05$) are in bold.

|	Warming		Acidification		Warming x Acidification	
	F	p	F	p	F	p
Top predator	110.76	**<0.001**	0.413	0.745	0.927	0.493
Mesopredator	9.15	**<0.001**	0.685	0.57	1.64	0.179
Herbivore	63.97	**<0.001**	7.03	**0.002**	2.14	0.086
Omnivore	80.72	**<0.001**	0.945	0.435	0.781	0.593
Detritivore	50.05	**<0.001**	0.761	0.527	4.2	**0.005**
Total zooplankton	61.32	**<0.001**	0.226	0.877	3.24	**0.018**
Green algae	4.83	**0.017**	9.03	**<0.001**	5.29	**<0.001**
Cyanobacteria	6.29	**0.006**	1.05	0.39	1.77	0.147
Diatom	35.99	**<0.001**	6.36	**0.003**	5.75	**<0.001**
Cryptophyta	4.82	**0.017**	5.94	**0.028**	0.635	0.7
Total phytoplankton	1.08	0.357	3.08	**0.047**	2.018	0.103

Table D.2: Results of two-way ANOVA testing the effects of predator removal, light reduction, and their interaction on the average densities of zooplankton and phytoplankton groups. All densities were log $(x+1)$ transformed for the analyses. Significant effects ($p < 0.05$) are in bold.

	Removal		Light		Removal x Light	
	F	p	F	p	F	p
Top predator	19.32	**<0.001**	1.23	0.308	1.04	0.404
Mesopredator	15.89	**<0.001**	0.403	0.673	2.17	0.099
Herbivore	2.68	0.087	1.14	0.334	1.15	0.356
Omnivore	0.118	0.889	0.921	0.41	0.53	0.717
Detritivore	3.13	0.06	9.35	**<0.001**	1.39	0.264
Total zooplankton	1.88	0.172	9.37	**<0.001**	1.03	0.409
Green algae	0.536	0.591	4.317	**0.024**	0.321	0.861
Cyanobacteria	0.346	0.711	18.7	**<0.001**	1.68	0.184
Diatom	0.818	0.452	0.726	0.493	0.296	0.878
Cryptophyta	0.964	0.394	23.17	**<0.001**	1.94	0.133
Total phytoplankton	0.29	0.751	3.78	**0.036**	0.485	0.746
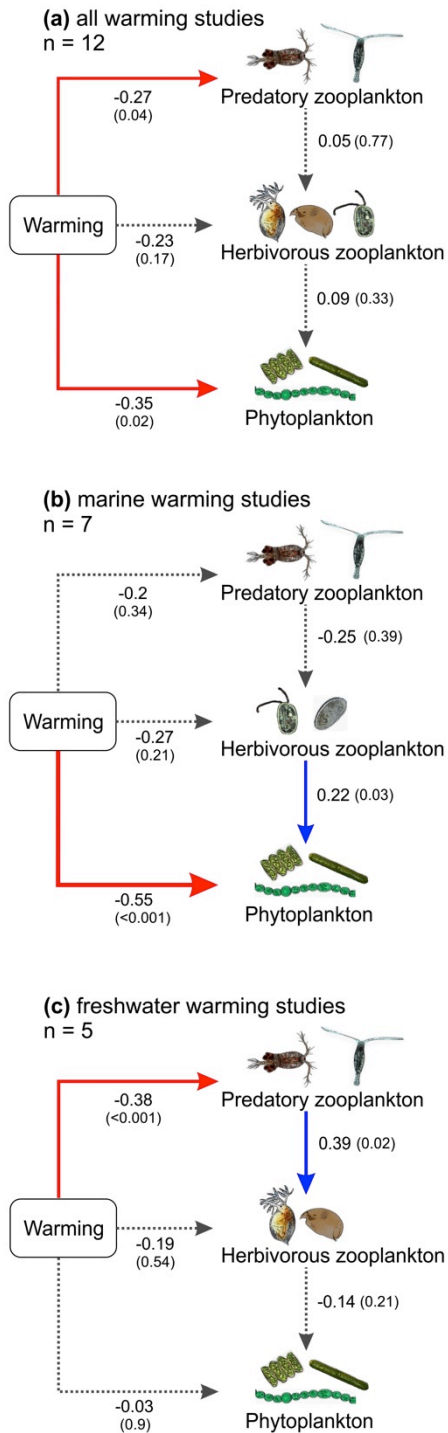
Figure D.1. Structural equation model meta-analysis results that include studies that significantly differ from a priori model. The path coefficients, which indicate the strength and direction of the relationship between variables, are shown above arrows with the corresponding p-values displayed in brackets. Bold arrows indicate significant negative (red) and positive (blue) relationships (p < 0.05) and dashed arrows indicate non-significant relationships.
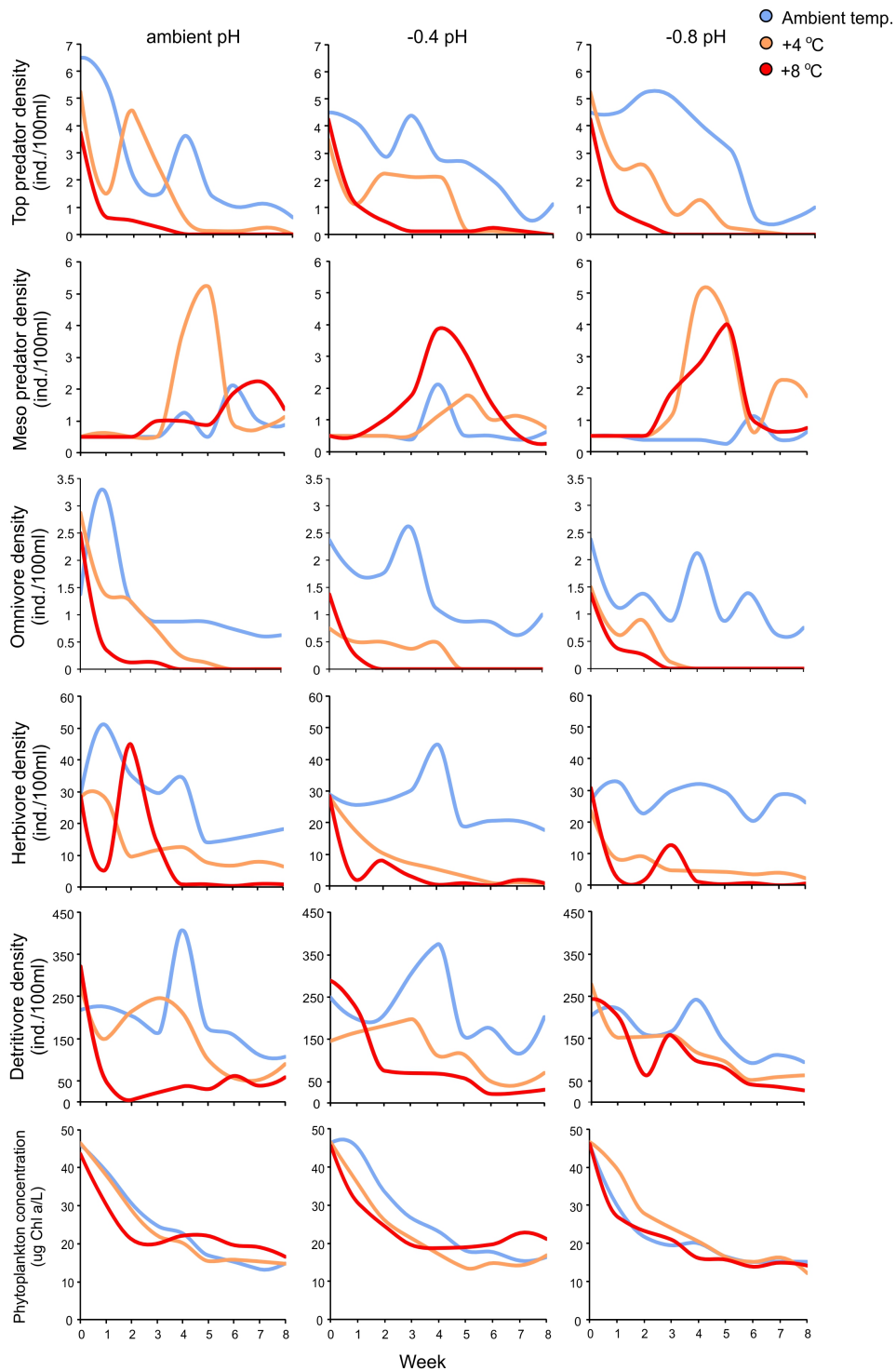
Figure D.2. Time trends of zooplankton trophic group density and total phytoplankton concentration in warming and acidification treatments. Interpolated time series for the average densities of each trophic group and average phytoplankton concentration (n = 4). Interpolation of each time series was performed using the Akima method.
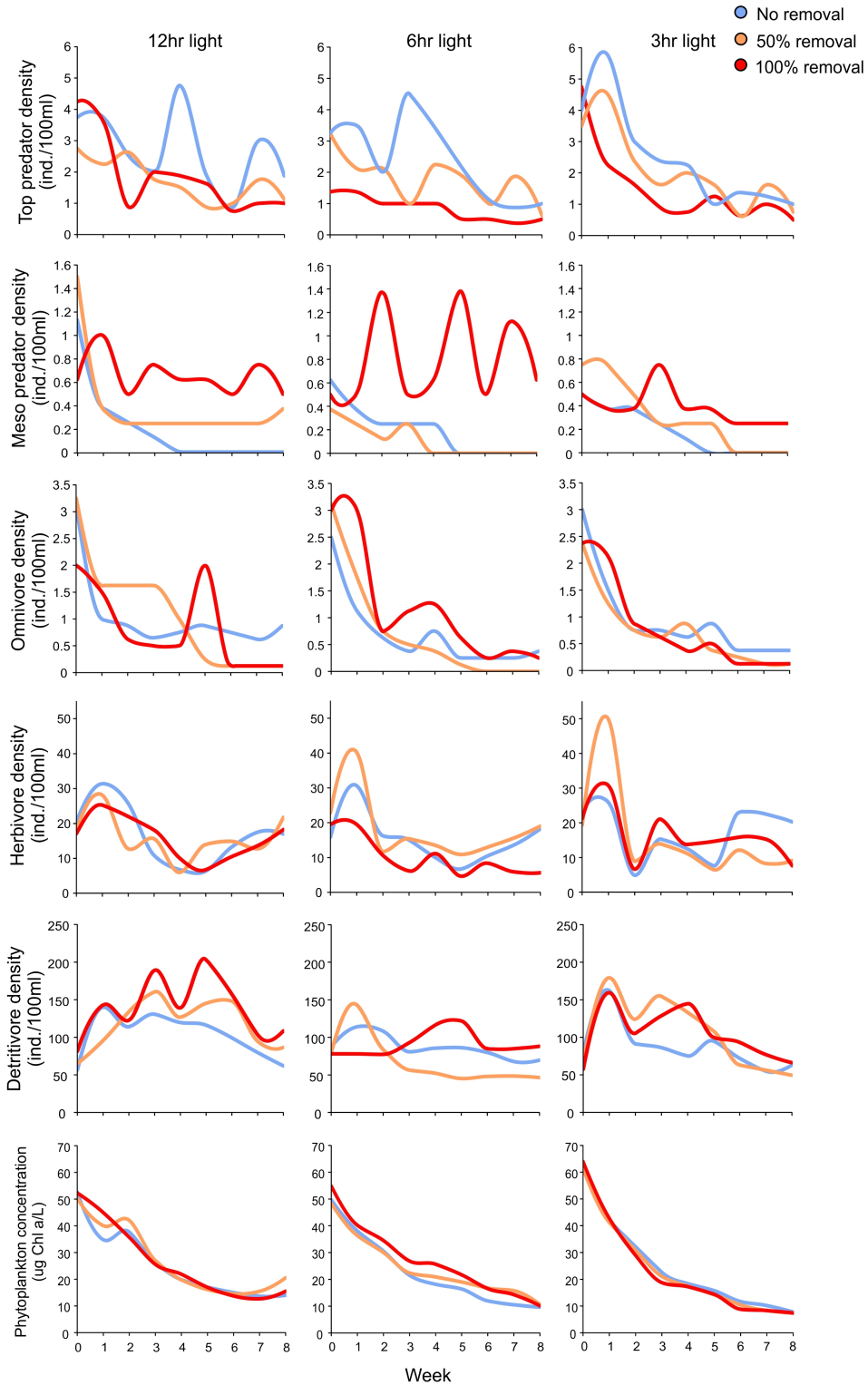
Figure D.3. Time trends of zooplankton trophic group density and total phytoplankton concentration in top predator removal and light reduction treatments. Interpolated time series for the average densities of each trophic group and average phytoplankton concentration (n = 4). Interpolation of each time series was performed using the Akima method.

117
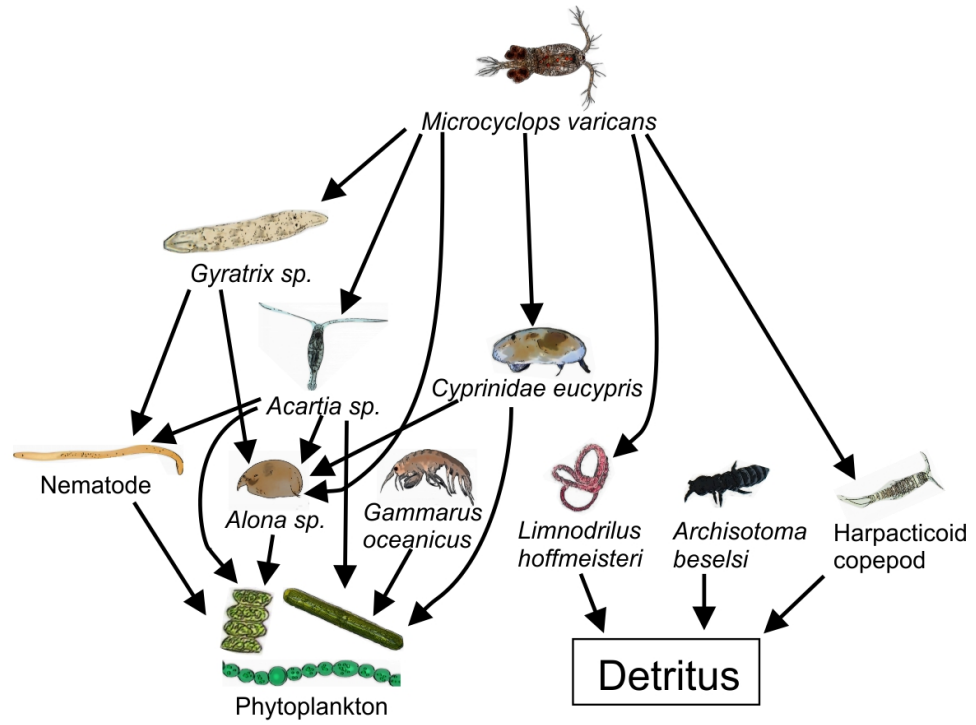
Figure D.4. Food web in experimental rock pool community. Arrows represent known feeding interactions.

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