UNIVERSITY OF CANTERBURY

DOCTORAL THESIS

Disentangling factors mediating diversity by modeling dynamics from populations to communities

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Abstract

Ecologists have worked for over a century to disentangle biotic and abiotic factors that regulate populations; I am no exception. Species interactions influence population dynamics by affecting abundance and distribution of species. Interactions form the backbone of foundation paradigms in ecology such as keystone species, trophic cascades, ecological niche, and community stability. Yet the bulk of understanding about interactions comes from pairwise interactions in simplified communities, likely missing processes and mechanisms that only emerge in diverse systems. These processes emerging in diverse systems may ultimately be responsible for maintenance of diversity seen in nature. Beyond interactions, several other factors may regulate populations and coexistence including heterogeneous environments, life-history traits, and the interaction of multiple ecological processes among members of the community. With the goal of improving our understanding of factors shaping the distribution, abundance, and diversity of natural communities, in this thesis I combined theoretical models and real-world data across three ecosystems. Specifically, for my first chapter I explored the relative roles of biotic and abiotic drivers of alpine plant communities at multiple scales. Here I found that individual populations responded to experimental treatments, while the whole community remained relatively constant suggesting weak treatment effects. Additionally, neither populations nor communities responded to the same drivers or in the same manner. I concluded that variable responses to these drivers allow some populations to persist and communities to remain stable as different species vary in response to the treatments. My second chapter focused on the role of facilitation and indirect interactions in an annual plant community. I found that both direct and indirect facilitation had measurable effects on annual plant fitness outcomes. I measured, for the first time in a natural system, the presence of 'native turncoats': native species indirectly facilitating introduced species. Indirect facilitative interactions may increase the fitness of some introduced species allowing them to succeed in spite of biotic resistance. In my third chapter, I focused on population dynamics of a space-limited community finding that it is structured by a competitive hierarchy but inferior competitors persist. I used inferred pairwise interaction coefficients to rank functional groups by competitive ability and used inferred recruitment to examine life-history trade-offs. I conclude that coexistence in this space-limited community is maintained by multiple, non-mutually exclusive mechanisms: trait differences acting as an equalizing mechanism, life-history trade-offs, and facilitation across a gradient of neighbor density. Together these projects provide insights into the various ways populations and communities are shaped by ecological processes. Cumulatively my work emphasizes the importance of quantifying variability and the diverse mechanisms that influence populations and ultimately the diversity of ecological communities.

Preface

This thesis is a collection of three stand alone scientific articles. These articles study the processes that influence population-dynamics and their implications for diversity of these systems. Each chapter is a standalone piece of research and, therefore, I only provide a general Introduction and Conclusion chapters linking the three research chapters together. In the General Introduction I focus on describing the state of the literature and the broad context from which my research questions originated. In the Conclusions, I focus on the relationship between each chapter's results and discuss the implications of this relationship for population-dynamics in diverse ecological communities.

At the time of submission, each of these three articles are in different stages of the publication process and are formatted in the style of a journal article. The first chapter, "Variable responses of alpine-plant communities to warming and loss of dominant species" will be submitted to Ecology Letters. The second chapter, "Enemy of my enemy contributes to success of introduced annual plants" will be submitted to Ecology. The third chapter, "Interactions and life-history trade-offs govern persistence in space-limited benthic communities" will be submitted to Ecology as well.

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Name: *Daniel B. Stouffer* Signature: Date: *2012-12-17*

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Part I

Disentangling factors mediating diversity by modeling dynamics from populations to communities

Chapter 1

General Introduction

Uncovering how species assemble into and coexist as a community is critical to understanding the diversity seen in nature. After more than a century as defining themes in ecology, community assembly and coexistence remain important areas of rich investigation (Darwin, 1859; Elton, 1927; Hutchinson, 1961; May and McLean, 2007). Recent advances in coexistence theory (Chesson, 2000b; Mayfield and Levine, 2010; HilleRisLambers et al., 2012; Chesson, 2018), the advancement of novel quantitative techniques (Ives and Helmus, 2011; Barabás et al., 2018; Ellner et al., 2019), and the recognition of diverse processes which govern ecological communities (Adler et al., 2006; Angert et al., 2009; Godoy et al., 2014; Levine et al., 2017a) have driven research in ecology in recent decades. Despite these advances, the question of: “what determines patterns of species diversity?" remains one of the big mysteries of ecology (Kennedy and Norman, 2005). Answering this question will have positive implications for endangered species conservation (DeCesare et al., 2010), the control of biological invasions (MacDougall et al., 2009), and predicting global climate change impacts (Chu et al., 2016). My research, therefore, strives to improve our understanding of factors that shape the distribution and abundance of populations and which ultimately allow for the diverse coexistence seen in nature.

Community assembly—where species from a regional pool disperse into a habitat and interact to form local communities—is a process operating at a range of spatio-temporal scales. Here, and for the remainder of this thesis, communities are defined as the association of populations of two or more species occupying the same area at the same time; while populations are a number of organisms of the same group or species who live in a particular area. The theoretical concepts of coexistence theory have allowed for the advancement of theory on community assembly, and many ecologists now cite a model of community assembly whereby communities are assembled via a hierarchy of nested processes from abiotic to biotic filtering (HilleRisLambers et al., 2012; Kraft et al., 2015). Sorting of species from the regional pool into local communities can reflect different physical tolerances which remove organisms unable to tolerate certain abiotic conditions or competitive hierarchies which favor organisms with traits that allow them to successfully compete for resources under given local abiotic conditions (Kraft et al., 2015) (Fig 1.1). Layered on top of this environmental filtering, is biotic filtering which shapes the final local community composition and diversity. In this thesis, biotic filtering refers to species interactions along the same trophic level at the scale of a community; however, species may be present or absent from a location due to multiple confounding mechanisms that would not be differentiated by describing biotic filtering as current species interactions (Kraft et al.,

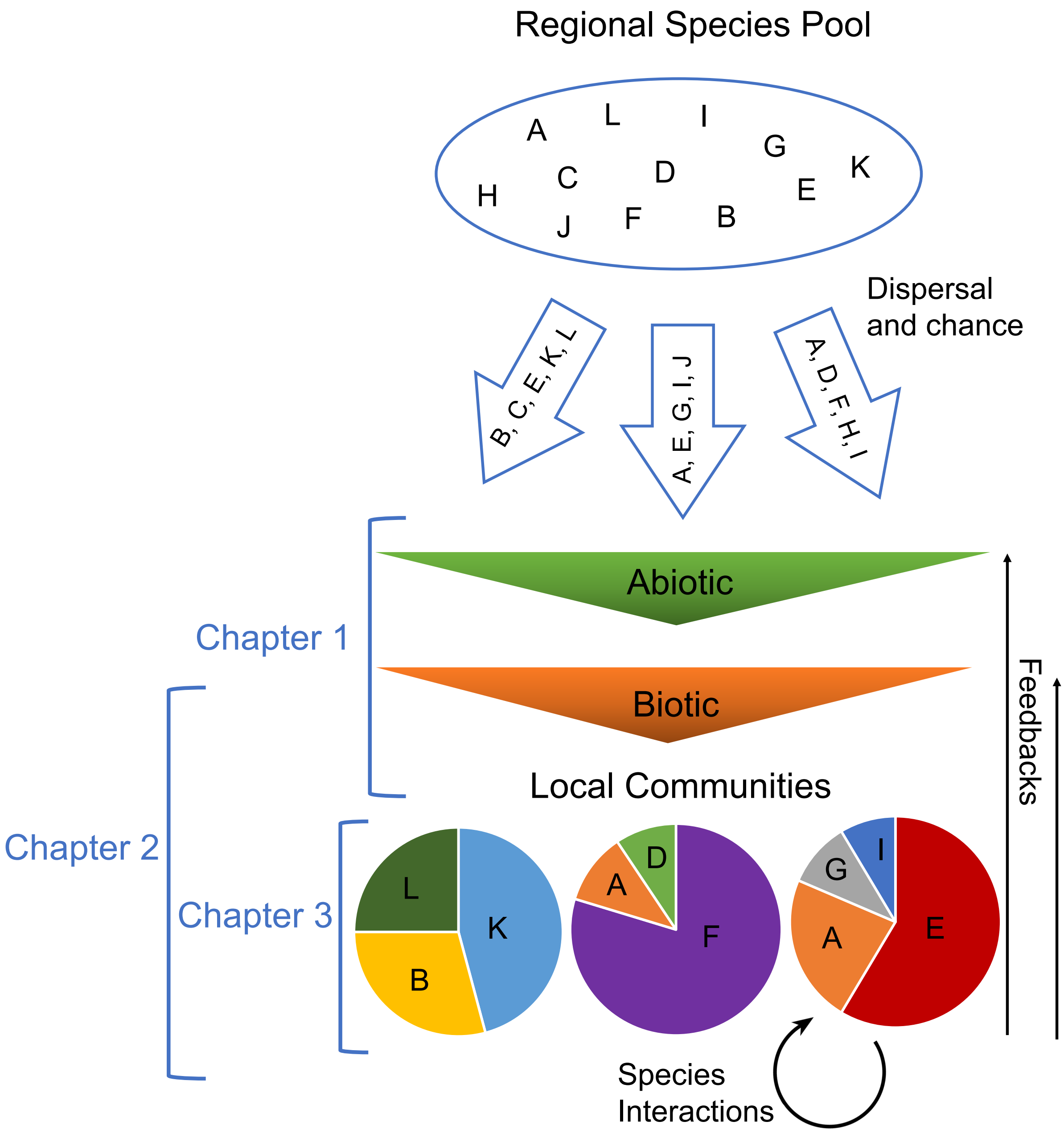

FIGURE 1.1: Conceptual figure of how community assembly and coexistence theory shape local communities from regional pools across a range of spatiotemporal scales. Community assembly is concerned with how a regional species pool is narrowed passing through abiotic (environmental) and biotic (interactions such as competition, predation, herbivory) filters to create a local community. While community assembly is often depicted as sequential filters and coexistence theory is most often concerned with local, current processes; in reality much of what is depicted in this figure may act simultaneously or feedback across the different spatiotemporal scales. Coexistence theory is generally aimed at understanding how local communities coexist through neighbor to neighbor species interactions and variations of the environment. Species interactions in the assembly context are distinguished from those in the coexistence theory context on the scale of the interaction where biotic filtering influences who can potentially live in a local community where my investigations into coexistence are concerned with the relative abundances of populations. In this thesis I focus on community- and population-level responses to abiotic and boitic drivers (Chapter 1); species interactions at the local community level and their influence on species entering those communities (Chapter 2); and species interactions and persistence within a local community (Chapter 3). These topics span both community assembly and coexistence theory to uncover factors that shape the distribution and abundance of populations. (Adapted from HilleRisLambers et al., 2012)

2015). For example, as species may be absent because it has not yet arrived at the location or may be present but has not yet gone extinct. While community assembly is often depicted as sequential filters in reality these processes may act simultaneously, as throughout the assembly of a community there are feedbacks between the abiotic and biotic processes (Germain et al., 2018). Species interactions may vary in their resulting outcomes within populations and across abiotic gradients (Thompson, 1988). For example, some mycorrhizal associations can be mostly mutualistic in infertile soil but antagonistic in more fertile soil depressing growth of their plant host (Bowen et al., 1980). This highlights the interplay between community assembly processes as the environment shapes species interactions and these interactions feedback into the biotic filtering.

Species interactions, both competitive and facilitative, are integral to explaining patterns of diversity. Estimating these interactions can lead to a greater understanding of complex processes leading to community stability and species coexistence (May, 1972; Ives et al., 2003). They can affect the abundance and distribution of species altering the overall structure of communities (Harpole and Tilman, 2006). Therefore, species interactions are the backbone of foundation paradigms in ecology such as keystone species (Paine, 1966, 1969) and trophic cascades (Estes and Palmisano, 1974) as well as theoretical concepts of the ecological niche, community stability, and competitive exclusion (Chesson, 2000b). One type of species interaction—competition—has arguably the longest-standing history in ecological studies of interactions and is often conceptualized as the key force structuring nature (Connell, 1961, 1972; Paine, 1966, 1969). The 'struggle for existence' view of the natural world dominates ecology (Darwin, 1859); however, recent research indicates the role of facilitation on population- and community-level variables is at least as important as other driving factors (e.g. Callaway, 1995; Stachowicz, 2001; Bulleri et al., 2016).

Facilitation is defined as an interaction in which one species enhances the growth, survival, or reproduction of a neighboring species (Bronstein, 2009). By incorporating positive interactions into broad ecological concepts, such as the niche, we can see that facilitation allows for a larger spatial extent of the realized niche than the fundamental niche (Bruno et al., 2003a). Classical examples of structure-forming foundation species are found in many ecosystems, including coral reefs, rainforests, kelp forests, and seagrass beds (e.g. Dayton, 1972; Estes and Palmisano, 1974; Orth et al., 1984; Witman, 1985), and these foundation species have been extensively studied for their facilitative interactions and roles in ecosystem functioning. Facilitation also plays a large part in succession, with early plants and trees modifying soil conditions to pave the way for subsequent extension of countless associated species (Crocker and Major, 1955). Despite many examples of facilitation and the influence it may have, incorporating positive interactions into ecological theory on community assembly and coexistence remains a challenge (Holland et al., 2002; Bimler et al., 2018). By understanding how species compete and facilitate within a community we can better understand how species can coexist in diverse communities.

Coexistence theory predicts that the species which can best compete for a common essential resource will drive the competitively inferior species to extinction (Tilman, 1982; Chesson, 2000a,b; Adler et al., 2007; HilleRisLambers et al., 2012). A community of species can stably persist because of multiple coexistence mechanisms operating among community members over long periods of time (Chesson and Warner, 1981; Chesson, 2000b, 2003; HilleRisLambers et al., 2012). Modern coexistence theory provides a useful conceptual framework that allows for quantifying the contribution of processes that shape ecological communities (Chesson, 2000b; Mayfield and Levine, 2010; HilleRisLambers et al., 2012; **?**; Adler et al., 2018; Petry et al., 2018). At its core, modern coexistence theory is built on models of pairwise species interactions among competitors, and the coexistence of these competitors depend on the relative importance of stabilizing mechanisms and fitness differences (Chesson, 2000b,a, 2003; Letten et al., 2017; Adler et al., 2018; Barabás et al., 2018). Stabilizing mechanisms cause a species to buffer its own growth when at high density more than it buffers growth of a competitor, and fitness differences describe differences in competitive abilities or growth rates among species (Chesson, 2000b, 2003; Levine and HilleRisLambers, 2009). Many mechanisms can lead to stabilizing mechanisms such as complimentary resource use (Tilman, 1994), differential responses to spatial and temporal environmental variation (Chesson and Warner, 1981; Angert et al., 2009), and species-specific effects of natural enemies (Paine, 1966, 1969; Connell, 1972; Janzen, 1970). Fitness differences reflect differences in resource use and can establish competitive hierarchies among species (Godwin et al., 2020). When stabilizing mechanisms become sufficiently strong to overcome fitness differences, long-term coexistence is possible (Chesson, 2000b). While this theory has led to a significant body of empirical work on measuring these processes, it is fundamentally pairwise and does not allow for the incorporation of facilitative interactions (but see Saavedra et al., 2017; Carroll et al., 2011).

Measuring species interactions and understanding factors that control their variability is essential for disentangling the complex biotic and abiotic factors impacting the structure of ecological communities. Historically, species interactions were simply qualified by their outcome (mutualistic, facilitative, competitive, parasitic) rather than quantification (Jackson and Buss, 1975; Jackson, 1979; Quinn, 1982; Schoener, 1983). Such categorization is insufficient to capture the full range of interaction effects, and more importantly, offers no insight into the relative importance of these effects (Thompson, 1988). As a result, ecologists have shifted to a more quantitative measure of interactions strength (Wootton and Emmerson, 2005). However, the majority of our understanding of species interactions and coexistence comes from pairwise investigations (e.g. May, 1972; Schoener, 1979; Chesson, 2000b; Freckleton and Watkinson, 2001). While practically these pairwise interactions are often simpler and more tractable to understand, this likely misses some processes that emerge when multiple species interact (Billick and Case, 1994). In the simplest case scenario with the addition of a third species, one can imagine that increasing density of limpets—inter-tidal grazers—indirectly increases the density of barnacles by removing algae which directly compete with barnacles for space (Dungan, 1986). This suggests that quantifying interactions among each pair of species in this system would be an oversimplification (Dungan, 1986) and would not capture the true measure of these species interactions. Since species rarely occur in only pairs in nature, quantifying interactions among the whole community can better represent processes controlling community structure as the presence of additional species changes the environmental conditions or modifies traits or behavior of the focal species (Wootton, 2002; Mayfield and Stouffer, 2017). Recent theoretical advances have allowed for the combined incorporation of pairwise and multispecies interactions into fitness models (Mayfield and Stouffer, 2017; Levine et al., 2017a; Kleinhesselink et al., 2019) providing more accurate measures. Despite these advances, there remain critical gaps in our understanding of community assembly and coexistence: how do species interactions (competitive and facilitative, pairwise and multispecies) regulate community persistence and stability.

My thesis aims to incorporate the variability of interactions into population dynamics models– examining both abiotic and biotic drivers, facilitation, and multispecies interactions– and improve our current understanding of ecological communities and their functions. Moreover, I aim to develop an understanding of how populations change under increased biotic and abiotic stressors such as invasions and global climate change. I accomplish this through three chapters: 1) the roles and interplay of biotic and abiotic factors that shape ecological communities, 2) the role of facilitation and multispecies interactions in diverse community persistence and invasion success, and 3) quantifying population dynamics and mechanisms of persistence in space-limited communities.

In Chapter 1, I examined the responses of alpine-plant communities to warming and loss of dominant species in order to better understand the roles and interplay of biotic and abiotic factors that shape ecological communities. Since communities likely respond to multiple drivers simultaneously and across multiple scales in nature, I use data from a global experiment to examine the population- and community-level responses of plant abundance to two drivers: warming and species removal. This global experiment took place in alpine plant communities across two elevations (low and high) at five locations (Canada, China, New Zealand, Switzerland, and United States). These sites featured a replicated experimental design that allowed me to understand the role of each driver in the community at large as well as the responses of individual species. I developed a discrete-time population-dynamics model to predict year-to-year changes in percent cover as a combination of density-independent and density-dependent changes. I designed these models so that they would enable us to separate community-wide (experimental plot level) responses from species-specific responses by estimating a grand mean parameter which represents the ‘average’ species in that community and estimating individual species deviations from this grand mean. I statistically fit this model to observed percent cover measurements using a Bayesian framework and then used a model-comparison framework to estimate the relative importance of each experimental treatment on alpine plant population dynamics. This study helps illuminate the role of abiotic and biotic drives on community persistence and stability.

To examine the role of multispecies interactions in diverse community persistence and invasion success, I examined annual plant communities in Chapter 2. Invasion ecology, like general ecology, often focuses on direct competitive interactions when measuring both the impact of and resistance to introductions. To broaden our understanding of multiple types of interactions, I measure how native species facilitate non-native species through an intermediate neighbor. The identity and location of each species within a plot were recorded at peak biomass, generating a complete, spatially explicit picture of the neighborhood in which all focal species grew. Given these data, I investigated the relative importance of direct and indirect species interactions on individuals' fitness. I examined 7.5 cm radius neighborhoods around each focal species to count the number of direct neighbors. I then applied this same 7.5 cm radius to those direct neighbors to find and count the focal's number of indirect neighbors. I inferred the strength of direct and indirect interactions by predicting fecundity as a function of direct and indirect neighbors. I statistically fit our fecundity models to observed fecundities for each focal species separately using a generalized linear mixed-effects model. This study provides insight into how facilitation and indirect interactions shape ecological communities.

In many space-limited systems, hierarchical organization patterns are the norm, where strict competitive hierarchies of species can be observed. As a result, it is assumed that the coexistence of these communities is maintained by predation or physical disturbance in order to prevent monopolization by one or few competitive dominants. However, these space-limited systems can be quite diverse in stable communities without significant disturbance. Therefore in Chapter 3, I investigated the factors allowing the persistence of and ultimately the diversity of space-limited systems. I examined the roles of interactions and life-history trade-offs in the persistence of multiple species in a space-limited community, using data collected in the benthic marine invertebrate community of Monterey Harbor central California, USA. I measured relative abundance of populations using experimentally assembled communities of species that co-occur widely. To quantify population dynamics parameters of growth rates, recruitment, and interactions, I developed a discrete-time population-dynamics model to predict year-to-year changes in cover of these organisms as a combination of density-independent and density-dependent changes. I used a Bayesian hierarchical mixed-effects approach where-by the cover was a function of previous cover and the effect of neighbors. All focal functional groups were fit simultaneously by allowing the effects of neighbors to vary for each focal through a random effect allowing for comparisons across groups. Disentangling the effects of species interactions and in turn patterns of persistence represents an important step in understanding the maintenance of diversity in space-limited systems.

Chapter 2

Variable responses of alpine-plant communities to warming and loss of dominant species

Abstract

The responses of ecological communities to perturbation are inherently variable because the responses of their constituent populations also vary. For example, species within a single study community may show combinations of no response, positive responses, and negative responses to any given perturbation. Here we explore the relative influence of direct and indirect impacts of climate change on alpine ecosystems in a global study. Specifically, we investigate the effects of warming temperature and species-loss treatments on population- and community-level dynamics across alpine-plant communities at two elevations in five globally-distributed mountain locations. Communities showed varied responses to both drivers, and no community showed unequivocal responses to a single treatment. Rather most sites showed support for both drivers since multiple models received WAIC weight. Populations within these communities responded idiosyncratically, suggesting that constituent species are not all equally robust to external perturbation even when community-level effects appear weak. Instead, our results highlight the challenge of making general predictions about population- and community-level patterns of common ecosystems in the face of present and future perturbations.

Keywords: Species interactions, Population dynamics, Global Change, Warming Experiment, Removal Experiment

Introduction

Environmental conditions and species interactions shape patterns of diversity and abundance under ambient conditions as well as influence how the resulting communities respond to environmental drivers. Temperature is one of the most fundamental drivers of biological patterns and processes, with temperature variability explaining much of the spatial and temporal patterns of distribution and abundance of species across the globe (Hutchins, 1947; Kordas et al., 2011). However, temperature is not the only can not predict where a species will live and how well it performs. Species respond directly to changing environmental factors (i.e. humidity and warming) based on individual- and population-level characteristics such as the way that their physiological tolerances limit their distribution (Grime, 1979; Huston, 1999; Pavoine et al., 2011). Although long recognized as biologically important, consequences of variation in environmental temperature have renewed importance as global climate change alters both mean and extreme temperatures. Additionally, species respond indirectly to environmental change as they respond to changes in the distribution, abundance, and/or behavior of natural enemies (competitors, predators, and parasites) and beneficial interaction partners (mutualists and facilitators) (e.g. Dunson and Travis, 1991; Davis et al., 1998; Sanford, 1999; Hawkins et al., 2009). General patterns in response to global climate change may be robust and predictable, yet accurate predictions of consequences of global climate change for a particular species or ecosystem are complicated by this interplay between direct and indirect effects (Kordas et al., 2011).

Elevation gradients represent a combination of co-varying abiotic factors, including temperature and soil moisture (Sundqvist et al., 2013), and thus can serve as natural experiments for studies on community and ecosystem response to long-term changes in climate (Sundqvist et al., 2013; McCain and Colwell, 2011; Pauli et al., 2014). High elevation plant communities, for example, are predicted to be strongly regulated by environmental factors (Grime, 1977) since they are often subject to more physically stressful conditions (Callaway, 1995). Interactions among species are also important drivers patterns in diversity and abundance across landscapes (Grime, 1979; May and McLean, 2007; Bruno et al., 2003a; Klein et al., 2004; Molau, 2010), and key interactions that are sensitive to temperature can act as "leverage points" amplifying small changes in climate into large consequences for the natural community (Sanford, 1999). Dominant species—those exerting strong control on the abundance and distribution of other species in the community (Weaver et al., 1938; Dayton, 1972; Paine, 1974a)—can have particularly large effects on the community by influencing the interactions among other species in many different ecosystems (Paine, 1969; Ellison et al., 2005). For example, high temperatures and physical stress set the upper limit of vertical zonation patterns in species' relative cover along temperate rocky shores, but competition for space from the competitive dominant *Mytilus* drives the seaward limit (Paine, 1966, 1969). In plants, *Empetrum nigrum* subsp. *hermaphroditum*—an evergreen dwarf shrub which dominates low-nutrient alpine ecosystems (Tybirk et al., 2000)—impacts other species by forming dense mats and producing allelopathic compounds (Nilsson, 1994). This in turn reduces germination and survival of co-occurring species, leading to reduced vascular plant richness (Aerts, 2010). Given the breadth of potential impacts, decreases in the abundance or complete loss of a competitive dominant can ripple through a community. This loss represents a direct impact of global climate change while other organisms respond indirectly as they are released from competitive impacts of the dominant and can devote more resources to growth or reproduction.

While there is an ever-growing body of literature that demonstrates the effects of warming temperatures (Wolkovich et al., 2012; Sundqvist et al., 2013) or species interactions (Adler et al., 2007; Brooker et al., 2008) on population- and community-dynamics, examining both drivers concurrently remains central to understanding how species coexist and how communities might respond to future environmental changes (Matías et al., 2018; Bimler et al., 2018). Moreover, change in an environmental variable could alter the cover of a species indirectly through species interactions (Adler et al., 2012), as interactions are known to vary in their outcomes and strength within populations and across environmental gradients (Bowen et al., 1980; Thompson, 1988; Bimler et al., 2018). For example, the effects of *E. nigrum* are found to be dependent on multiple environmental variables as its influence in mediated through soil moisture and geomorphic disturbance (Mod et al., 2014). Recent work within annual-plant communities has shown that interactions between plants may shift from competitive to facilitative along environmental gradients (He et al., 2013; Badano et al., 2007; Bimler et al., 2018). This indirect response to the environment stems from species-specific responses to the environment, which can change the absolute or relative cover of the interaction partners or the relative strength of interactions themselves (Adler et al., 2009; Bimler et al., 2018). As a result, the interplay of environmental conditions and species interactions remains an important piece of the puzzle as modified species interactions can lead to differing conclusions about the dynamics and stability of whole communities (Suttle et al., 2007).

Previous studies have explored variation in plant responses to experimental warming and composition manipulation with mixed results (e.g. Hobbie et al., 1999; Rixen and Mulder, 2009; Cavieres and Sierra-Almeida, 2012) because the scales measured among experiments varied. One way forward is to measure population- and community-level responses to these drivers through coordinated experiments at multiple sites. Therefore, we examine the response of plant cover to direct effects of climate change through warming treatments and indirect effects of climate change through a species removal treatment in alpine communities across two elevations (low and high) at five locations (Canada, China, New Zealand, Switzerland, and United States). We aimed to quantify how individual populations of alpine plants within multiple experimental plots responded to a biotic and an abiotic driver. These ten sites featured a replicated experimental design to understand the role of each driver in the system at large as well as the responses of individual species. We chose this system because alpine systems, and alpine-plant communities in particular, are extremely sensitive to temperature increases since they already exist along a gradient of increasing physical stress with increasing elevation (Klanderud and Totland, 2008; Walther et al., 2005; Venn et al., 2012). Thus they act as good indicators for predicting how climatic changes through temperature changes or shifting species interactions will impact plant species globally (Dullinger et al., 2004). Moreover, while individual alpine species are geographically isolated and restricted to high-elevation areas (Grabherr et al., 1994), this type of community exists globally allowing for studies that cross latitudinal gradients which may offer insight to broad-scale population-dynamic patterns. We use experimental treatments as alternative hypotheses of the relative importance of abiotic and biotic drivers in determining percent cover of alpine-plants. We expected that the effect of species removal would be greater than the direct effect of warming, as these communities may experience a range of temperatures and are long-lived allowing them to buffer against extremes. High elevations are temperature limited while intensity of competitive interactions is greater at low elevations, therefore, we expect the impact of species removal to be greater at low elevations. Additionally, we expect variation among locations in the effects of warming and removal due to inherent differences and co-factors such as water availability.

Methods

Field Methods

The data used here come from the WaRM (Warming and (species) Removal in Mountains) project which consists of replicated field surveys completed at high and low elevations within the alpine communities among five locations in Canada (CA), China (CN), New Zealand (NZ), Switzerland (CH), and United States (US) (abbreviated using their two letter ISO code, Table A.1). Henceforth, we will refer to specific elevations within a location as "sites". At each elevation, the experiment consisted of eight replicate blocks, containing 2 m × 2 m square plots with 2 m buffers. Plots were randomly assigned to one of four treatments: ambient control (hereafter ambient, A), ambient temperature with dominant removal (hereafter removal, R), warmed without removal (hereafter warmed, W), and warmed and dominant removal (hereafter warmed and removal, R:W). This resulted in 32 total plots per site. Removal treatments consisted of above-ground biomass removal of the locally dominant species, repeated yearly, by clipping to ground level (and, as necessary, application of herbicide). The locally dominant species was the same for all plots at a given site, and these species were not included in percent cover measurements used in the analyses described below (see Appendix A 'Dominant Species' for more details). Warmed plots consisted of open top chambers covered with hexagonal polycarbonate with sloping transparent sites and an inside diameter of 1.5 m which stayed in place during the growing season and achieved an increase of 1-3 °C during this time (Henry and Molau, 1997; Molau and Mølgaard, 1996) (Fig A.1). For the warmed and removal treatment, removal took place over the 2 m × 2 m plot while the warming encompassed 1.5 m diameter within that. During the growing season, annual sampling within each plot consisted of visual percent-cover estimates from the center of each plot to monitor changes individual species cover and changes in composition within the plot. There are five sampling years in US and CH, and four sampling years at the other three sites. However, the CN treatment plots were not measured explicitly for all years in the study (i.e. some were measured in years 1, 2 and 3 but not year 4, or other combinations), and this lead to lower replication at this site. All plants within a plot were recorded to the lowest taxonomic unit available with supplemental laboratory identifications as needed. We made our best effort to use accepted nomenclature and consistency in species names throughout the study period in each location (Table A.5). Non-vascular plants such as mosses were included in the analysis. Mosses were only observed in low elevation CH plots and accounted for an average cover of 7.57%.

Population-Dynamics Model

We aimed to quantify how individual populations of alpine plants within the experimental plots responded to the aforementioned biotic and abiotic drivers. We thus developed a discrete-time population-dynamics model to predict year-to-year changes in percent cover of these plants as a combination of density-independent and density-dependent changes (Rees et al., 1996; Adler et al., 2012; Martorell and Freckleton, 2014). We designed our models such that they would enable us to separate community-wide (experimental plot level) responses from species-specific responses by estimating a grand mean parameter which represents the 'average' species in that community and estimating individual species deviations from this grand mean. Specifically, we estimated percent cover $N_{i,t}$ of a focal species i in the current year as a function of the prior year's percent cover $N_{i,t-1}$ with a model that takes the general form

$$N_{i,t} = Q_i + N_{i,t-1}\, e^{G_{i|R,W}} \tag{2.1}$$

where Q_i represents density-independent increase in percent cover (influx), which may be attributed to recruitment, lateral encroachment into the plot, and/or plants emerging from the seed bank. Note that this Q_i term is not influenced by previous percent cover. Mathematically this helps us account for observations of a species that were unobserved in the previous year, which occurred in 42% of our observations (see Appendix A for site-specific observations). Since experimental plots were randomly assigned throughout the landscape, we assumed that this density-independent influx of species was equal and unaffected by the treatments. In contrast, the model component $N_{i,t-1}e^{G_{i|R,W}}$ captured density-dependent changes in percent cover since it is multiplied by previous percent cover; these changes can be driven, for example, by growth or mortality. We constrained our model so that it would never predict non-biologically-plausible negative percent cover by constraining Q_i to be positive and calculating the exponential of $G_{i|R,W}$.

In order to separate community-wide from species-specific responses in density-independent change in percent cover, Q_i of a species i is given by a combination of common and species-specific deviations of the form:

$$Q_i = \frac{0.5}{1 + e^{-(q_{common} + \Delta q_i)}} \tag{2.2}$$

Q_i is constrained with 0.5 as a maximum to be more biologically plausible and improve model fit. The combination of the community-wide grand mean (q_{common}) and the species-specific deviations (Δq_i) can be interpreted as the inferred density-independent change in percent cover for that species.

We likewise parameterized density-dependent change $G_{i|R,W}$ of a species i such that it contained both the common and species-specific effects, but here we allowed these effects to also vary as a consequence of the experimental treatment. Mathematically, this takes the form:

$$G_{i|R,W} = g_{\text{common}|R,W} + \Delta g_{i|R,W} = (g + \Delta g_i) + R(g_R + \Delta g_{R_i}) + W(g_W + \Delta g_{W_i}) + RW(g_{RW} + \Delta g_{RW_i})\,, \tag{2.3}$$

where the parameters R (removal) and W (warming) equal 1 in plots where that treatment was applied and otherwise equal 0. The species-specific responses for each species i under each treatment were captured as deviations from these grand means via the parameters Δg_i, Δg_{R_i}, Δg_{W_i}, and Δg_{RW_i}. The combination of the community-wide grand mean and the species-specific deviations can be interpreted as the inferred density-dependent change in percent cover for that species. For example, the estimate of $g_{\text{all}|R} = g + g_R$ can be interpreted as the component of density-dependent change of the 'average' plant at a given site under the removal treatment while the estimate of $\Delta g_{i|R} = \Delta g_i + \Delta g_{R_i}$ indicates how species i deviates from this grand mean.

Model Inference

To estimate the relative importance of each experimental treatment on individual alpine plant population dynamics, we statistically fit this model to observed percent cover measurements. Since our main goal is to identify the importance of drivers to individual alpine plants, we chose to investigate each location and elevation separately. Additionally the community composition varied both between high and low elevations at the same location and among locations further supporting the decision to handle each site (location × elevation) independently in our analyses. We also concentrated our analysis on the most widespread species within each site (Figs A.2 and A.3, determined as the species observed in at least 25 percent of total plots; for example, 0.25 × 32 plots × 4 years = 32 plots, which becomes the minimum number of plots a species must be present in to be analyzed). The resulting number of plots varied by location since the CH and US sites were sampled for five consecutive years while the other locations were sampled for four years (Table A.1). Widespread species represent those that tend to be pervasive and abundant. We tested the robustness of this threshold, and found that fitting the model to species in 20 and 30% of plots showed qualitatively consistent results at the site level (results not shown). While these widespread species represent a subset of the total species observed, they account for the majority of the percent cover observed in the plots (Table A.2, Figs A.2 and A.3).

We used a Bayesian hierarchical model with Hamilton Markov Chain Monte Carlo (HMCMC) methods to infer the parameter values of our model which best reproduced the observed percent cover dynamics of each focal species (Eqs 2.1 & 2.3). Rather than estimate each species' deviations from the grand mean (Δ parameters) as separate fixed effects, we parameterized these deviations in a comparable manner to how random effects are included in mixed-effects models. Doing so enabled us to estimate how each species responded to the treatments, and this parameterization helped in providing estimates for each species that are pulled towards the grand mean when its sample size is low (McElreath, 2016). Our Bayesian, two-level hierarchical model for our dynamic model of year-to-year variation in cover of a focal species i within a sampled plot may be written as:

$$N_{i,t} \sim \text{Beta}(\lambda_{i,t}, \phi, z_i) \tag{2.4}$$

$$\lambda_{i,t} \sim Q_i + N_{i,t-1} e^{G_{i|R,W}} \tag{2.5}$$

$$Q_i \sim \frac{0.5}{1 + e^{-(q_{common} + \Delta q_i)}} \tag{2.6}$$

$$\{q_{common}, g, g_R, g_W, g_{RW}\} \sim \text{Normal}(0, 10) \tag{2.7}$$

$$\{\Delta q_i, \Delta g_i, \Delta g_{R_i}, \Delta g_{W_i}, \Delta g_{RW_i}\} \sim \text{Multivariate Normal}(\sigma, \rho) \tag{2.8}$$

$$\sigma \sim \text{HalfCauchy}(0, 2) \tag{2.9}$$

$$\rho \sim \text{LKJcorr}(2) \tag{2.10}$$

$$\phi \sim \text{Gamma}(0.01, 0.01) \tag{2.11}$$

$$z_i \sim \text{Beta}(1, 1) \tag{2.12}$$

where $\lambda_{i,t}$ refers to the mean predicted percent cover of species i in year t.

We used a zero-inflated beta distribution to simulate predicted percent cover. A beta distribution is appropriate for percent cover data as it is ideal for continuous data and allows for a flexible shape (U-shaped, L-shaped, etc.) (Wright et al., 2017; Damgaard and Irvine, 2019). We used weakly informative priors to parametrize the treatment (control, R, W, and RW) terms within growth (Eqn 2.7) since we had no previous knowledge with which to constrain these parameters. In our Bayesian approach, we incorporate constraints on parameters through the use of priors, which act as a set of values (distribution) that the parameter is believed to fall within and may represent prior knowledge or belief about the parameter. Here our weakly informative priors help the Markov chains' convergence and stabilization while still letting the data speak by excluding various 'unphysical' possibilities that would otherwise take over the posterior distribution (Gelman, 2009). The Markov chains work to estimate the posterior distribution for each parameter; this distribution represents the knowledge of the parameter after observing the data.

We defined varying effects of each focal species, that correspond to deviations from the grand mean (Δ parameters), with a non-centered parametrization of a multivariate normal distribution (Gut, 2009a) with a mean (σ) and covariance matrix (ρ) between the varying effects for each species (Eqn 2.8). We used weakly informative priors of half Cauchy for the mean and LKJcorr(1) for the covariance matrix (Eqn 2.9-2.10) (McElreath, 2016). The Cauchy distribution is a thick-tailed probability distribution; in this case, a half-Cauchy (restricted to positive values) acts as a weakly informative/regularizing prior for standard deviations (McElreath, 2016). The LJKcorr distribution of correlation coefficients provides a weakly informative prior on the covariance matrix which is skeptical of extreme correlations near -1 or 1 (Lewandowski et al., 2009). This implies that our model is skeptical of extreme correlations between the species since we wish to allow each species to respond to treatments individually.

We performed sampling to determine the posterior distributions of model parameters with the function "brm" from the package "brms" (Bürkner, 2017) in the statistical program R (version 3.4.2) (R Core Team, 2013). We ran two chains with a warm-up of 1000 iterations and 4000 sampling iterations each, and these produced a final combined posterior of 6000 MCMC samples for each model. We determined that parameters converged when trace plots were well mixed and stationary, and when the Gelman-Rubin convergence diagnostic was close to one (Gelman and Rubin, 1992; Brooks and Gelman, 1998). A stationary chain shows a path that stays within the posterior distribution, close to a central tendency for the length of the chain (McElreath, 2016). A well-mixed chain means that each successive sample is not correlated with the previous sample, leading to a rapid zig-zag pattern (McElreath, 2016) whereas the Gelman-Rubin convergence diagnostic (Rhat) far above one generally indicates that a chain has not converged (Gelman and Rubin, 1992; Brooks and Gelman, 1998).

Model Comparison

At each site (location × elevation), we compared a series of six models (developed in a step-wise fashion from least-parameterized to most) to examine the relative importance of each treatment or treatment combination to variation in population dynamics (Table 2.1). Here our models serve as alternative hypotheses for describing the year-to-year changes in percent cover of alpine plants. Therefore, our main motivation is to determine which model has the best predictive accuracy, and hence is expected to fit future observations well, rather than assessing which model is correct (Aho et al., 2014). The Null model ($N_{i,t} = N_{i,t-1}$) predicts percent cover as a function of previous percent cover ($N_{i,t-1}$, if Q_i and G_i are zero) and acts as a well-defined baseline for comparison. The Recruitment model modifies this null model to include density-independent change in percent cover (influx, Q_i), resulting in $N_{i,t} = Q_i + N_{i,t-1}$. The Ambient model measures density-independent change in percent cover (influx, Q_i) and density-dependent change in percent cover in absence of any treatment effects ($N_{i,t-1}e^{g+\Delta g_i}$, Table 2.1).

Building on this, the single-treatment models (Removal and Warming) modify density-dependent change in percent cover by adding the main effect of the corresponding treatment (Table 2.1). The Removal + Warming model includes the main effects for both treatments but without an interaction term (Table 2.1); and the final, Removal × Warming model, contains the main effect of both treatments and their interaction (Table 2.1). We used the Widely Applicable Information Criteria (also known as Watanabi-Akaike Information Criterion: WAIC) to determine the best model or models for each elevation (Watanabe, 2010; Burnham and Anderson, 1998). Similar to other information criteria (e.g. AIC, DIC), WAIC provides a measure of model fit that is penalized for the number of model parameters, and a lower value signifies a better model fit. We examined other information criteria finding that they were consistent with WAIC in most cases (data not shown); therefore, we only discuss WAIC for the model-selection process. We also used Akaike weight (based on WAIC) to compare the relative predictive accuracy of models, where larger values indicate greater support (Burnham and Anderson, 2002a; McElreath, 2016). We defined best-fit models as those with the lowest WAIC and an Akaike weight greater than 0.8; when a single model did not meet this criteria, we used model averaging to combine models' posterior distributions based on Akaike weights.

Results

Total percent cover in experimental plots remained similar over the course of the experiment and did not vary with treatment (Fig A.4). In Canada (CA) and Switzerland (CH), most plots showed no difference between final and initial percent cover at the community-level. United States (US) plots increased in percent cover, and New Zealand (NZ) plots showed variable

TABLE 2.1: Model names and their density-dependent components which we compared for each site. Model parameters are as outlined in Eq (2.3).

Model name	Density-dependent change in percent cover, $G_{i\|R,W}$
Null	0
Recruitment	0
Ambient	$g + \Delta g_i$
Removal	$g + \Delta g_i + R(g_R + \Delta g_{R_i})$
Warming	$g + \Delta g_i + W(g_W + \Delta g_{W_i})$
Removal + Warming	$g + \Delta g_i + R(g_R + \Delta g_{R_i}) + W(g_W + \Delta g_{W_i})$
Removal × Warming	$g + \Delta g_i + R(g_R + \Delta g_{R_i}) + W(g_W + \Delta g_{W_i}) + RW(g_{RW} + \Delta g_{RW_i})$

results (Fig A.4). While percent cover in plots varied across locations and elevations, treatment was not a significant predictor of percent cover (Table A.3). China (CN) was not used in this analysis as it had too few replicates of the same plot measured in both the final and initial years. For more details see Appendix A (Linear Regression Analysis).

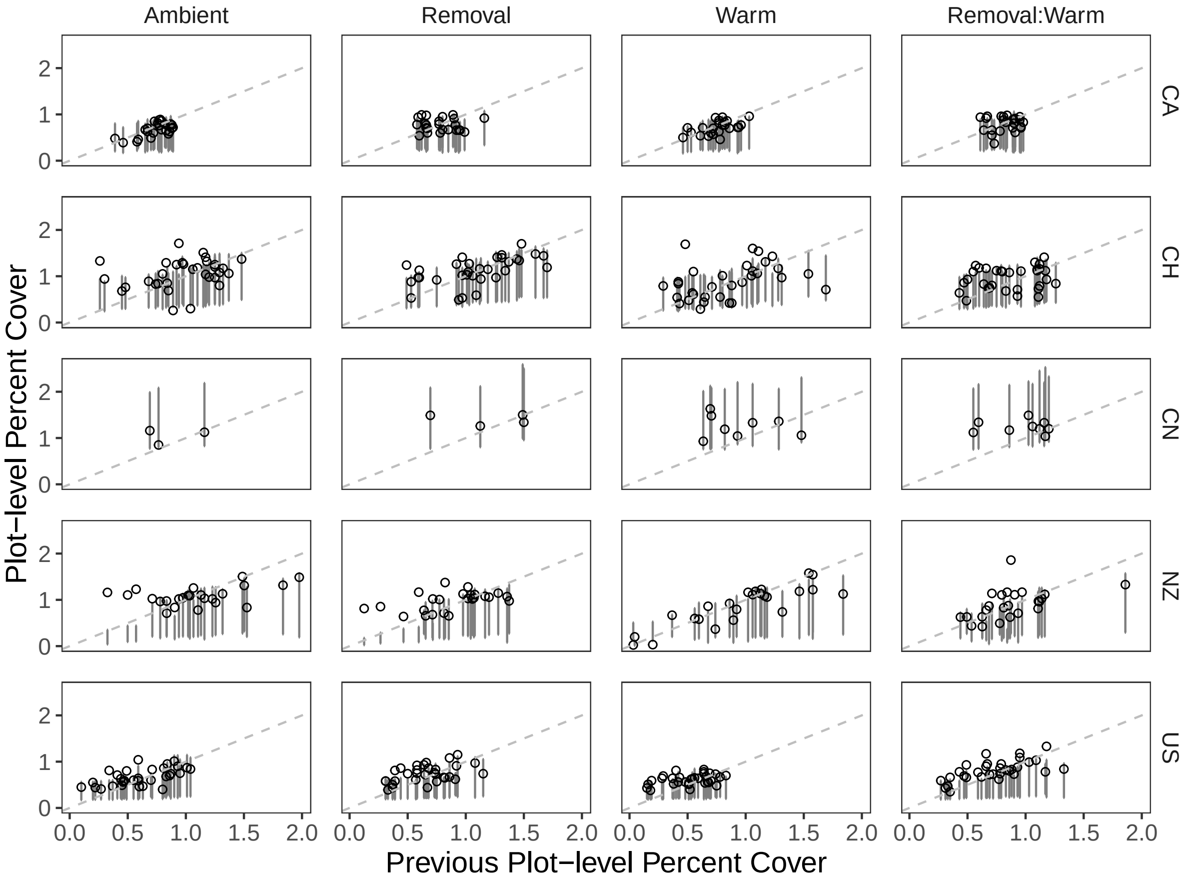

FIGURE 2.1: Year-to-year total percent cover for all plots at low elevation across all sites. Points show the total observed percent cover in a plot while vertical lines show the credible interval (89%) of our statistical model's predicted total percent cover for that plot. Species-specific predicted percent cover is calculated according to Eqn 2.1 then summed across all species within a plot to yield predicted plot-level percent cover. As a visual guide, the dashed line represents the 1:1 or where previous percent cover would equal current percent cover (i.e. when total percent cover in a plot neither increases nor decreases). Comparable plot for high elevation can be found in the Appendix A.

We statistically fit population-dynamics models to observed data to examine the effects of different drivers (climate warming and removal of the dominant species) on year-to-year changes in the percent cover of particular alpine plant species. Our population-dynamics models fit well across a range of locations, observations (Fig 2.1, species richness values (between 7-26 per site), and plant species identities (Fig 2.1) despite low sample size at some sites. In general, our population dynamics model predicts increases in year-to-year percent cover when previous percent cover is low and decreases when previous percent cover is high leading to abundances remaining relatively constant (Fig 2.1.

Our model formulation using a random effect for species allowed us to separate the dynamics at the community-level or the 'average' species from the dynamics of individual species. This process allows us to better understand which experimental treatments affected each scale independently. Below we present these results separately to highlight the different scales of inference achieved with this model formulation.

Population Dynamics

Community-Level Results

While we fit our model to observations of individual plant species, we can scale up to get a sense of what is happening at the plot-level; here 70% (664 out of 946) of observed plot-level percent cover were within the predicted credible intervals (Fig 2.1). Additionally, examining the grand mean of a community gives a picture of how the 'average' species responded to treatments, but as we will see later these communities are made up of many species that themselves respond to treatments idiosyncratically. In general, communities remained relatively stable with predicted percent cover (a combination of density-dependent and density-independent changes) similar to previous percent cover suggesting small differences from $N_{i,t}$ to $N_{i,t-1}$. This was true for communities at both elevations (low elevation Fig 2.1; high elevation Fig A.5) and supported by both our population-dynamics models and statistical linear models (see Appendix A Linear Regression Analysis for more detail).

Despite the commonalities shared across the various locations studied, the best-fit models varied among locations (CA, CH, CN, NZ, and US) and even by elevation (High vs. Low) within a location, highlighting the complicated nature of communities, especially in responses to multiple perturbations. Three sites (high elevation CH, low elevation NZ, and low elevation US) showed no obvious effect of treatments with the Ambient model receiving all the WAIC and Akaike weight support (Table 2.2). The remaining seven sites had mixed support for different models. Four of these sites (low elevation CA, low elevation CH, high elevation NZ, and high elevation US) showed support for treatment effects with a treatment model gaining $>50\%$ of WAIC weight (Table 2.2). High elevation US was the only site that showed majority support for warming while low elevation CA showed majority support for the removal treatment. Both low elevation CH and high elevation NZ showed some support for both treatments. High elevation NZ showed additional support for the warmed and removal treatment model. In general, median inferred growth under treatments was an order of magnitude lower than median inferred growth under ambient conditions suggesting weak treatment effects. While

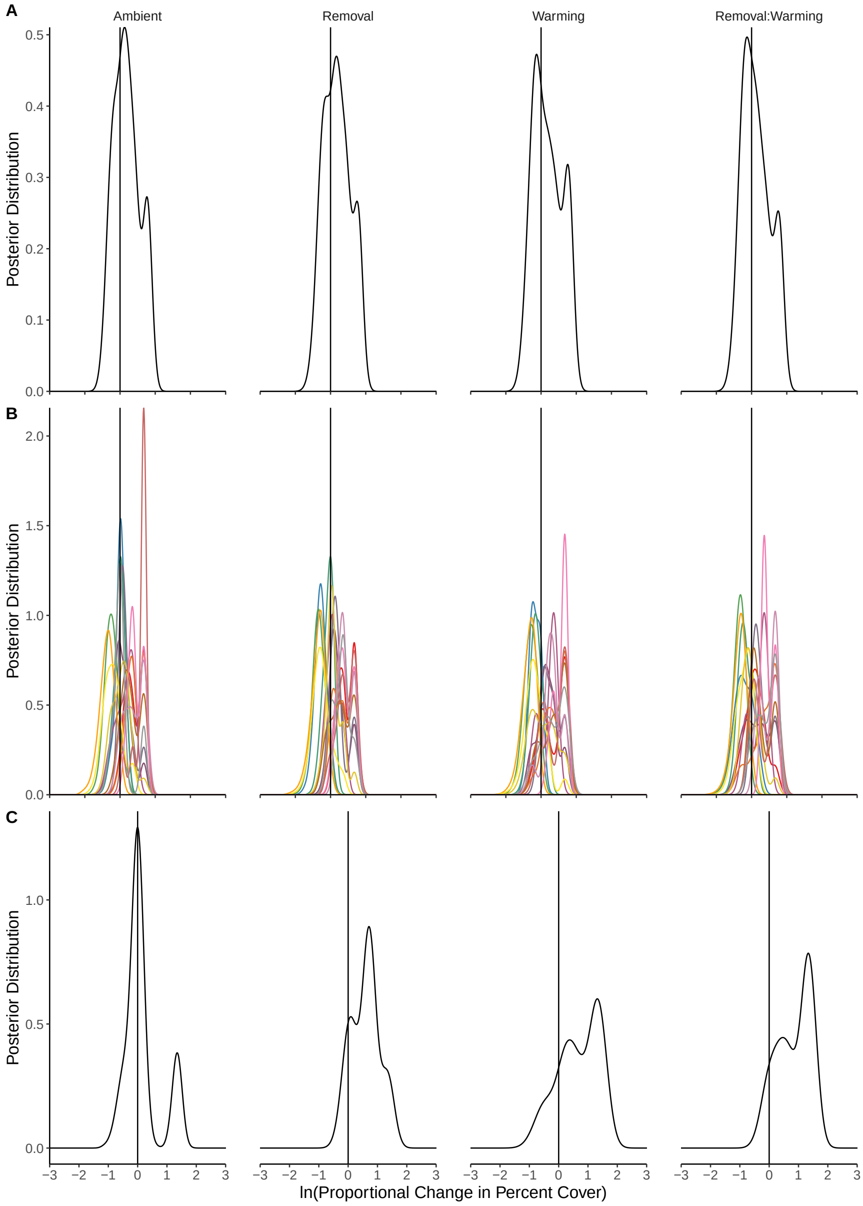

FIGURE 2.2: Posterior distribution of predicted logarithmic proportional change in cover within the low elevation Canada site based on the predictions of the best-fit model. This site acts as a representative example of the variable responses to treatment we observe at the species-specific level. Logarithmic proportional change in cover is calculated as ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}})$) as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. A) Shows the posterior predictions based on the community-level grand mean or the 'average' species, which in this case only shows minor effects of the removal treatment. B) Shows the posterior predictions for all species at this site illustrating how species vary within and among treatments. C) Shows the changes in a single species *Veronica wormskjoldii*. This species showed an increase in density-dependent change in cover with the removal of the dominant species compared to the values near zero under ambient conditions. Warming and the Removal*time*Warming treatments did not receive any model support at this site so their predictions reflect the ambient and removal predictions, respectively. Since this metric includes observed previous percent cover, differences seen in unsupported treatments reflect variations in species percent cover rather than inferred parameters.

variable in nature, this suggests that the models are capable of capturing a community-level percent cover response to treatments when it is present.

Given the diversity of species in this system, many individual species had low percent cover estimates in a given plot during a given sampling suggesting that this prediction of increase will be common and offset others that may decline when their percent cover is high allowing plots to generally remain consistent in percent cover. To envision how our models predict percent cover, we can take an example of low elevation CA. If the 'average' species had a previous percent cover of 10%, the model estimates its percent cover in the following year to be 3.06% in the ambient plots, 3.16% in removal plots, and 2.81% in warming plots. This median estimate is made up of both the density-independent and density-dependent factors. Density-independent influx alone predicts the next year's percent cover to be 0.044%. On the other hand, the median estimate of density-dependent change in percent cover in the ambient treatment is $g = -1.20$ (Table 2.3). To understand the meaning of this value, we exponentiate it and then multiply it by previous percent cover ($N_{t-1} \times e^{g_{common}} = 10\% \times e^{-1.20} = 3\%$). At this site, multiple treatment models received support (Table 2.3). In the removal treatment, the median density-dependent change ($g_{common} + g_{R_i}$) in percent cover was estimated as $e^{(-1.20+0.05)} = 0.316$ as this treatment adds to the value from the ambient estimate. This leads to predicted percent cover of 3.16% for our example scenario, suggesting that removal of the dominant species slightly helped the 'average' species in this community compared to the ambient control. In contrast, the warming treatment lowered percent cover of the 'average species' compared to ambient plots suggesting that this community was vulnerable to the direct effects of warming ($e^{(-1.20-0.07)} = 0.28$. Consider high elevation CH as another example. If the 'average' species there had a previous percent cover of 10%, the model estimates its median abundance in the following year to be 3.63% in the ambient plots. This predicted percent cover is made up of density-independent influx (q_{common}) of 0.0326% and a density-dependent component of 3.6% with this site showing support for the ambient only model. If the 'average' species instead had a previous percent cover of 1%, the model estimates its abundance would decrease in the following year to 0.39% in all the plots.

TABLE 2.2: Model comparison table giving information criteria for each model tested for low and high elevation communities in Canada (CA), Switzerland (CH), China (CN), New Zealand (NZ), and the United States (US). WAIC (Widely Applicable Information Criteria) penalizes models for parameters and the lowest WAIC reflects the best-fit model. pWAIC is the effective number of parameters and provides information on how flexible each model is in fitting the sample. Weight refers to Akaike Weight for each model. This weight can be interpreted as an estimate of the probability that the model will make the best predictions of new data compared to a set of models considered. Low elevation NZ recruitment model did not converge and is not listed below.

Location	Elevation	Model name	WAIC	pWAIC	Weight
CA	Low	Removal	-1012.33	24.91	0.64
		Removal + Warming	-1009.80	27.35	0.19
		Ambient	-1008.63	18.99	0.10
		Removal × Warming	-1007.08	29.52	0.05

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Location	Elevation	Model name	WAIC	pWAIC	Weight
		Warming	-1005.57	22.18	0.02
		Null	-893.31	4.94	0
		Recruitment	-712.11	4.29	0
	High	Ambient	-114.04	11.38	0.55
		Warming	-112.97	12.14	0.32
		Removal	-110.13	12.81	0.08
		Removal + Warming	-108.44	12.95	0.03
		Removal × Warming	-107.13	12.04	0.02
		Null	82.35	4.62	0
		Recruitment	152.42	6.07	0
CH	Low	Removal + Warming	-1254.80	28.22	0.61
		Removal	-1263.06	23.65	0.26
		Removal × Warming	-1260.45	30.17	0.07
		Ambient	-1259.56	17.54	0.04
		Warming	-1257.67	22.89	0.02
		Null	-1170.57	5.23	0
		Recruitment	-976.63	4.64	0
	High	Ambient	-2964.51	29.49	0.87
		Removal	-2959.28	34.12	0.06
		Removal × Warming	-2958.43	49.90	0.04
		Warming	-2957.40	34.74	0.02
		Removal + Warming	-2952.74	38.94	0
		Null	-2644.70	6.92	0
		Recruitment	-2487.47	12.56	0
CN	Low	Ambient	-1506.36	28.01	0.73
		Removal	-1502.81	30.94	0.12
		Warming	-1502.26	30.61	0.09
		Removal + Warming	-1499.95	32.80	0.03
		Removal × Warming	-1498.99	34.10	0.02
		Null	-1354.89	4.14	0
		Recruitment	-1222.02	15.55	0
	High	Removal + Warming	-769.00	15.54	0.22
		Removal	-768.98	15.51	0.22
		Warming	-768.96	14.90	0.21
		Removal × Warming	-768.82	15.57	0.20
		Ambient	-768.30	15.25	0.15
		Null	-605.07	3.92	0
		Recruitment	-495.79	9.16	0

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Location	Elevation	Model name	WAIC	pWAIC	Weight
NZ	Low	Ambient	-6179.09	70.27	0.96
		Warming	-6172.69	79.47	0.04
		Removal	-6167.75	81.04	0
		Removal + Warming	-6163.84	89.43	0
		Removal × Warming	-6152.03	98.12	0
		Null	-5732.963	15.41	0
		Recruitment	-	-	-
	High	Removal × Warming	-904.69	27.33	0.63
		Warming	-903.27	24.13	0.31
		Removal + Warming	-899.42	27.02	0.05
		Removal	-896.76	23.29	0.01
		Ambient	-895.43	20.24	0.01
		Null	-797.26	9.15	0
		Recruitment	-696.81	7.33	0
US	Low	Ambient	-2457.85	25.26	0.88
		Warming	-2452.78	30.04	0.07
		Removal	-2452.01	29.74	0.05
		Removal + Warming	-2447	34.68	0
		Removal × Warming	-2443.08	38.57	0
		Null	-2170.14	6.06	0
		Recruitment	-1926.82	9.16	0
	High	Warming	-3163.72	29.58	0.70
		Ambient	-3161.50	24.99	0.23
		Removal + Warming	-3158.53	34.29	0.05
		Removal	-3155.53	29.88	0.01
		Removal × Warming	-3154.40	38.01	0.01
		Null	-2894.53	5.79	0
		Recruitment	-2753.39	10.12	0

While no site showed exclusive support for the Warming model, multiple sites showed marginal support for including this treatment based on Akaike weights (high elevation CA, high elevation CN, high elevation NZ, and high elevation US, Table 2.2). Specifically, the Warming model accounted for 70% of the Akaike weights in the high elevation US model comparison (missing our 80% cutoff for a winning model, Table 2.2). While it did not show exclusive support for warming, warming did have a small positive effect on the community (Table 2.3). If we again use our example of the 'average species' with a previous percent cover of 10%, the predicted percent covers are 7.9% in ambient plots and 8.65% in warming plots. High elevation US showed a larger increase in percent cover (0.75%) with treatment compared to our earlier example of low elevation CA which saw a 0.2% decrease in percent cover under warming. Additionally, multiple sites showed some support for the interaction treatment (Removal × Warming), with this model receiving approximately 5% WAIC weight. In high elevation CN, the Removal × Warming model received 20% WAIC weight; however, this site showed mixed support for all treatment models with them receiving an equal split of the weight possibly due to the low sample size at this site.

While there was support for a measurable influx of new species into plots, our model differentiated this from how species already present in the communities were responding to treatments in terms of variation in their density-dependent change in percent cover. At the community-level, median estimates of year-to-year density-independent influx of species also varied by site ranging from $q = -3.93$ to $q = -1.81$ amounting to 0.009 and 0.070 percent cover respectively. Species in low elevation NZ received the lowest average contribution of this influx to variation in species percent cover and low elevation CH received the highest contributions (Table 2.3). Density-independent influx may have resulted from an influx of seeds, germination of seeds from the seed bank, or lateral encroachment of neighboring plants which may be allowing plots to maintain equilibrium percent cover, given density-dependent change in percent cover ($e^{g_{common}}$) of less than 1 in some areas.

Species-Specific Results

Communities in this study were composed of varying amounts of species which differed not only in their initial percent cover but also in their density-dependent change in percent cover and dynamic responses to treatments. Though the effects of treatments were not always apparent at a community-level scale (Fig 2.1 and Figs A.6–A.14), our models were able to detect many impacts at the species-specific scale. Indeed, some of the statistical support for including or removing the different treatment effects may be due to differences across species in addition to any signal that was detected at the community scale. This notion is supported further by the observation that species on the whole responded idiosyncratically to treatments within each site. That is, there were species in each site that exhibited responses similar to, more exaggerated than, or contrary to the grand mean density-dependent change in percent cover (Figs 2.2 and A.6–A.14). Within each site, species responded idiosyncratically. For example, at low elevation CA, the community-level grand means showed support for the inclusion of the removal treatment but with a small effect on grand mean density-dependent change in percent cover (Fig 2.2). Within this site, species showed variable predicted changes in logarithmic proportional change in cover ($ln(N_{i,t}/N_{i,t-1})$) under ambient conditions and the same species showed different yet equally variable changes in percent cover after the removal of the dominant species (Fig 2.2). Under ambient conditions, six species showed a mean change in percent cover of near zero suggesting that they remained close to their previous percent cover and are near equilibrium. After the removal of the dominant species, an additional species within this site showed no proportional change in their percent cover and remained at equilibrium in the absence of the dominant. Three species that were near equilibrium under ambient conditions experienced a positive change in percent cover after the removal of the dominant. This suggests that some species increased their density-dependent change in percent cover in absence of the dominant compared to their growth under ambient conditions (Fig 2.2B). On the other hand, one species showed a decrease in percent cover moving away from equilibrium. Specifically, one species, *Veronica wormskjoldii* showed an increase in median percent change in cover with the removal of the dominant species compared to ambient conditions (Fig 2.2C). This result differed from the 'average species' proportional change in cover seen at this site (Fig 2.2). Warming treatment at low elevation CA had similarly variable results with only one species showing no change. Overall species increased (4), decreased (3), or showed no change (9) compared to ambient conditions. This site acts as just one example of the number of different dynamics observed at the species-specific level, see Appendix A for addition sites (Figs A.6–A.14).

Discussion

Here, we explored the relative roles of direct and indirect effects of global change on alpine-plant communities across multiple locations and elevations using a combination of empirical data and population-dynamics modeling. We found that most communities did not show unequivocal responses to our experimental manipulations (Table 2.3), and the percent cover of these communities remained relatively constant (Figs 2.1 and A.5) suggesting overall "resistance" to treatments at the community level. This pattern of no or weak treatment effects was seen in both our main population-dynamics model (Fig 2.1) and additional linear analysis (Fig A.3, refer to Appendix A for results). The relative importance of dominant species removal and warming temperatures varied among communities, with four out of the ten communities studied showing moderate support (low elevation CA, low elevation CH, high elevation NZ, high elevation US) for treatments with varying inferred effects of warming and removal of the dominant. While no community showed unambiguous support for treatments as a predictor of change in percent cover, high elevation US showed limited support for the effects of warming, and low elevation CA showed limited support for removal of the dominant (Table 2.3). Beyond these general patterns, species within a community showed variable responses to experimental disturbances, as some responded similarly to the 'average' species at their site given by the grand mean while others deviated strongly from this average (Fig 2.2). These species-specific responses, possibly due to varying life-history strategies of alpine plants (i.e. forb compared to C3 graminoid), may allow the overall community to persist in the face of environmental change even as some individual populations decline (Pauli et al., 2014). However, we did not detect any strong responses of individual growth forms (see Appendix A for more detail, Table A.5). Our results highlight the complicated nature of uncovering how drivers of population dynamics will be altered by the scale of the observation (community- vs. population-level; single- vs. multi-site) as well as by future and on-going disturbances such as climate change.

At the community-level, we observed small changes in percent cover in response to biotic, abiotic, and biotic × abiotic drivers. The dominant species at each site were from a variety of functional groups (e.g. C3 graminoids, herbs, and woody shrubs) which did not dictate the remaining species' response to the loss. Additionally, functional diversity of the remaining species also did not appear to dictate the importance of the treatments or their response to treatments (see Appendix A for more detail, Tables A.5 and A.4). In our experiment, the removal treatment offers insight into the role played by dominant species and captures the response of remaining species. While we did not detect a shift in the importance of neighbors (i.e. the dominant species) through our model comparisons, we can see a shift in the influence of the dominant species among elevations which is consistent with the stress-gradient hypothesis (Bertness and Callaway, 1994; Callaway, 1995; He et al., 2013). For example, removal was somewhat important at the low elevation in Canada (64% of WAIC weight) but less so at the high elevation there (8% of WAIC weight). Here, we inferred higher percent cover (less density-dependent decrease) in removal compared to ambient treatments in low elevation communities suggesting previously negative (competitive) interactions with the dominant. High elevation CA communities on the other hand showed a decrease in percent cover with the loss of the dominant suggesting the dominant has facilitative effects. There was a similar pattern among elevations in China. Low elevation China communities increased in percent cover while high elevation communities decreased in response to removal, though again with limited support for the removal treatment model. Small changes in total percent cover at the community level did not imply that these communities were robust to perturbations. Indeed, responses of the subdominant species were mixed suggesting that the dominant species, while influential, did not interact with all species equally or in the same manner (Fig 2.2). For example, low elevation Canada communities contained some species that were sensitive to and others that were resistant to the removal of the dominant species. On the other hand, high elevation Canada communities contained species that were more resistant to the removal of the dominant species. Previous work highlights that even small changes in the relative biomass of abundant species can cascade into large effects on ecosystem functioning (Grime, 1998; Gaston and Fuller, 2008). Thus even with limited community-level effects (small changes in percent cover) at some sites, the loss of the dominant species could lead to a shift in ecosystem functioning because remaining species vary in percent cover resulting in changes in above- and below-ground primary productivity and other ecosystem functions (Liu et al., 2018).

Beyond biotic drivers, alpine systems can be extremely sensitive to temperature (Erschbamer, 2007). Despite overall trends in responses to environmental changes, some studies (including ours) find variable responses to warming (see Henry and Molau, 1997; Erschbamer, 2007; Elmendorf et al., 2012). A global review found that warming had positive effects on graminoid species abundance at cool sites but had neutral or negative effects at warm sites (Elmendorf et al., 2012). In our study, experimental warming influenced few communities, with only marginal support and limited effects on percent cover at the high elevation United States suggesting that warming alone might be less influential to these communities at least over short (<5 year) time scales. Our study also differs from some previous studies as we did not add ambient temperature of each year as a predictor or covariate in our model, and using ambient temperature as a covariate may have illuminated some effects of warming (Elmendorf et al., 2012). In addition to direct impacts on individuals, if the direction or magnitude of response to temperature varies among species, a change in temperature can also alter species interactions (Kordas et al., 2011). Our results also suggest that both abiotic and biotic drivers had effects on alpine-plant communities in low elevation Switzerland and high elevation New Zealand.

For example, in high elevation New Zealand, which showed support for the interaction treatment, if the ‘average’ species had 10% previous percent cover in the warming treatment this species would drop to 5.18%, and species in the removal treatment would slightly increase to 5.61% compared to ambient plots at 5.39%. In the combined warming and removal treatment at this site, the same ‘average’ species would have 4.76% showing a more pronounced decrease in percent cover when both factors are combined. This was the only site in our study which showed support (through model comparison) for the Warming × Removal treatment suggesting that, while each disturbance alone had impacts on some plant communities, they rarely seem to interact. This runs contrary to both our original expectation of synergistic effects and to some previous studies, such as one in Finland where community composition modulated the effects of climate change on an alpine-plant system (Shevtsova et al., 1997; Virtanen et al., 2010). Nonetheless, this pattern of community composition modulating the effects of climate change is not consistent across experiments from different regions. For example, Hobbie et al. (1999) concluded that global warming may not alter species interactions since they found no interaction between warming and species removal in tussock communities in the Alaskan tundra. Clearly, the response of alpine-plant communities and the role biotic and abiotic factors play in shaping those communities, is context-dependent.

As we saw here, community-wide responses suggest one trend while species within these communities respond idiosyncratically to biotic and abiotic drivers. We found that the loss of the dominant species and experimental warming in these alpine-plant communities can have a variety of effects on the remaining community depending on species identity and location. While this result may not be novel to those familiar with the system (Pauli et al., 2014; Erschbamer, 2007), our results can help reconcile previous conclusions by demonstrating that alpine-plant communities may broadly differ in the drivers structuring their communities. A pressing future challenge will be to understand the biological reasons behind these patterns of community- and species-specific responses to abiotic and biotic disturbances, the combination of the two, or none of the above. Therefore, we suggest that future studies focus on this overlapping role of biotic and abiotic disturbances in similar communities to determine if and how this pattern is affected by community composition. We also point to short- and long-term responses as an avenue for future research as we did not yet have the data to explore how these patterns may be affected by the time-scale of the study. Our results represent a relatively short time scale (<5 years) which may show short-term responses to global climate change but may be too short to uncover patterns in long-term responses of communities. Previous warming experiments have drawn variable conclusions that are difficult to synthesize since studies often differ in the length of time or have varying responses throughout the length of a single study (Elmendorf et al., 2012; Kremers et al., 2015; Chapin III et al., 1995). As long-term data sets, such as this one, continue to grow, they offer opportunities for fruitful research ventures into different temporal and observational scales (species, community, and functional-group levels). While we saw that removal of the dominant species was important for the remaining species at one site and the direct impacts of warming influenced the community at another, we did not aim to find a common response with sites as replicates. However, questions about a common response could be investigated by comparing functional groups with sites as replicates, at the expense of species-level inferences. Though a major conclusion of 'it depends' might feel unsatisfactory, in reality, it points to the complicated and multifaceted determinants of population dynamics in diverse ecological communities.

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TABLE 2.3: Median estimates from the posterior of model parameters. Note that these are untransformed and hence correspond to Eq 1 and 2. High elevation CN, low elevation NZ, and high- and low-elevation Switzerland represent composite models based on Akaike weights; therefore, do not have Rhat values.

Location	Elevation	Model Name	Parameter	Estimate	Lower 0.95	Upper 0.95	Rhat
CA	Low	Composite	q	-2.33	-2.44	-2.21	-
			g	-1.20	-1.36	-1.03	-
			g_R	0.05	-0.13	0.22	-
			g_W	-0.07	-0.18	0.03	-
CA	High	Composite	q	-2.18	-2.58	-1.83	-
			g	-0.34	-0.70	0.02	-
			g_R	-0.04	-0.31	0.24	-
			g_W	-0.24	-0.51	0.03	-
CH	Low	Composite	q	-1.812	-1.94	-1.68	-
			g	-0.71	-1.02	-0.44	-
			g_R	0.04	-0.05	0.24	-
			g_W	-0.04	-0.14	0.05	-
			g_{RW}	0.15	0.01	0.31	-
CH	High	Ambient	q	-2.66	-2.93	-2.35	1.01
			g	-1.02	-1.42	-064	1
CN	Low	Composite	q	-1.81	-1.94	-1.67	-
			g	-0.79	-1.02	-0.60	-
			g_R	0.14	0.02	0.26	-
CN	High	Composite	q	-2.66	-2.76	-2.57	-
			g	-1.01	1.14	-0.88	-
			g_R	-0.09	-0.14	-0.04	-
			g_W	-0.005	-0.05	0.05	-
			g_{RW}	0.06	-0.05	0.18	-
NZ	Low	Ambient	q	-3.93	-4.29	-3.58	1
			g	-0.63	-0.87	-0.41	1
NZ	High	Composite	q	-3.70	-3.93	-3.49	-
			g	-0.62	-0.84	-0.42	-
			g_R	0.04	-0.09	0.18	-
			g_W	-0.04	-0.16	0.11	-
			g_{RW}	-0.26	-0.47	-0.02	-
US	Low	Ambient	q	-2.61	-2.90	-2.33	1
			g	-1.12	-1.52	-0.63	1
US	High	Composite	q	-2.32	-2.43	-2.21	-
			g	-1.05	-1.16	-0.95	-
			g_W	0.18	0.12	0.26	-

Chapter 3

Indirect interactions contribute to success of introduced annual plants

Abstract

Invasion ecology, like general ecology, often focuses on direct competitive interactions when measuring both the impact of and resistance to introductions. Variability in invasion risk is a central question in invasion ecology leading to hypotheses about how direct, antagonistic interactions prevent introductions. Yet, experimental and observational studies offer conflicting insights. Positive, indirect interactions between residents and introduced species in an 'enemy of my enemy is my friend' situation may provide an explanation for these conflicting conclusions. Generally, this is examined in the context of 'invasional meltdown' where introduced species facilitate the invasion of other introduced species. Instead, here we examine how native species may be leading to increased introductions by quantifying 'native turncoats', native species indirectly facilitating introduced species. We investigated the presence of indirect positive interactions and the impact of these interactions on individual fitness of species among a diverse annual-plant system. We statistically fit annual plant fecundity models to each individual species' observed seed sets in order to infer the effect of neighbors on an individual's fitness (as measured by seed production). We separated the effects of direct and indirect neighbors using a spatially explicit dataset of observed seed production. We measured direct neighbors as plants within a 7.5 cm diameter neighborhood of a focal plant while indirect neighbors were plants within a 7.5 cm diameter neighborhood of the direct neighbor. Interactions with these neighbors decreased or increased a focal species' seed production (fecundity), representing competition or facilitation respectively, compared to the focal species' intrinsic seed production or production in absence of neighbors. We define 'native turncoats' as a native indirect neighbor that increase an introduced species' seed production. We fit the fecundity models to the observed seed production of each of 20 focal individuals to estimate the effects of direct and indirect neighbors on individual fecundity. Of the 770 inferred direct and indirect interactions across all species, 347 (45%) were facilitative ($\alpha_{ij} < 0$)). This method of classifying indirect neighbors based on native status highlights the interactions with a generic native or introduced species rather than specific individual species. We detected the presence of 'native turncoats' in one of the five introduced focal species and in this case the enemy of your enemy had particularly large effects, increasing fecundity of this focal species in the presence of indirect native neighbors. In the remaining introduced focal species, we did not detect an overall facilitative effect from a native indirect neighbor but this does not rule out 'native turncoats' that are canceled out by strong competitors. We measured, for the first time in a natural system, the presence of 'native turncoats': native species indirectly facilitating introduced species. These results highlight the need to include indirect and positive interactions in our understanding of communities' resistance to introduced species.

Keywords: Indirect interactions, Facilitation, Invasion Ecology, Native turncoats

Introduction

Variability in invasion risk was originally explained by Elton (Elton, 1958) as biotic resistance: the ability of species-rich systems to safeguard themselves from invaders, as high diversity of native species leads to stiff competition which introduced species cannot overcome (Fox and Fox, 1986; Marchetti et al., 2004). Several hypotheses suggest that direct, antagonistic interactions should strengthen a community's resistance to invasions, but results from experimental and observational studies designed to examine invasion success offer conflicting conclusions (Sax and Brown, 2000; Keane and Crawley, 2002; Davies et al., 2005; Fridley et al., 2007). Experimental studies—those that directly manipulate diversity and invasion pressure—regularly show reduced invasion success with increased native species diversity (e.g. (Tilman, 1997; Stachowicz et al., 1999; Levine, 2000; SP. et al., 2004; Hooper et al., 2012; Naeem et al., 2012)). Diverse communities that include strong competitors or predators are thought to be particularly difficult to invade, and there is likely to be a negative correlation between native species richness and invasion success through direct competition for limited niches (Shea and Chesson, 2002). In contrast, various observational studies have shown the opposite (e.g. (Marchetti et al., 2004; Fridley et al., 2007)) and often attribute this to variable biotic and abiotic conditions that increase niche availability and the likelihood that every species will ultimately find favorable conditions (Espinosa-García et al., 2004; Davies et al., 2005; Gilbert and Lechowicz, 2005). Despite these equivocal results, biotic resistance has become one of the leading paradigms of invasion biology (Sax and Brown, 2000) leading to the continued search for general patterns and mechanisms to predict risk of invasions to a system.

Previous studies of biotic resistance focus on direct competition within simplified communities and often overlook positive and indirect interactions between multiple species that could better explain biotic resistance, or lack thereof, observed in natural systems. Facilitation generally increases biodiversity (Northfield et al., 2015), and ecosystem functioning (Bulleri et al., 2016). However, the main focus of facilitation research in invasion ecology has been in the context of the 'invasional meltdown' hypothesis (Simberloff and Von Holle, 1999), where introduced species facilitate the invasion of more introduced species. Less attention has been given to native–introduced species facilitation: the facilitation of native species by exotic invaders or vice versa (but see (Lucero et al., 2019)). Among the few studies that examine native–introduced facilitation some find that native foundation species such as habitat or structure formers of mussels in beds or trees of a forest, can increase the abundance (Bruno, 2001; Lenz and Facelli, 2003), population growth (Griffith, 2010), and spatial distribution (Altieri et al.,

2010) of introduced species. While these studies highlight facilitation between native and introduced species, they are also restricted to direct facilitation, even though facilitation is mediated through competitive loops and other indirect interactions (Mayfield and Stouffer, 2017; Northfield et al., 2015). Even fewer studies are devoted to understanding how indirect interactions mediate biological invasions. We aim to fill this gap by studying indirect interactions and their influence on introduced species.

Indirect interactions, where one species benefits or harms another by directly affecting an intermediate species, are common and ecologically important in shaping many types of communities (Connell, 1983; Northfield et al., 2015). Numerous studies have found that two species sharing a third competitor can mediate indirect facilitation, which results from a network of competitive interactions. This scenario is sometimes referred to as 'the enemy of my enemy is my friend' (Aschehoug and Callaway, 2015). Species may also indirectly benefit each other indirectly by harming or benefiting an intermediate species, for example, one species competing with a parasite or predator of another (Levine, 1999; Allesina and Levine, 2011), one species may be host to a species which forms a mutualism with another species (Beggs, 2001), or one species may benefit another which is the host to a parasitic species (McKinney et al., 2009). Northfield and colleagues (Northfield et al., 2015) recently extended this thinking of indirect interactions to the context of invasion ecology. They showed that the probability of successful introductions into a community increased as the numbers of resources and of species increased due to what they termed 'native turncoats': resident species that have indirect facilitative effects on an invading species by directly altering the abundance of the introduced species' enemy (e.g. competitor, predator, or parasite) (Fig 3.1). The presence of 'native turncoats' may explain the paradox of invasions as larger, more diverse communities are more likely to include indirect interactions and by chance, a proportion of those would be expected to be facilitative. Therefore, the objective of this study is to determine the prevalence of 'native turncoats' and indirect facilitation in natural communities.

To explore the empirical prevalence of 'native turncoats', we examined naturally occurring annual plant communities in SW Western Australia's York gum–jam woodlands. While 'native turncoats' (Northfield et al., 2015) originally referred to population-level dynamics, we frame the investigation as native neighbors indirectly facilitating introduced focal species through an intermediate neighbor (Fig 3.1). Based on previous studies in this community (Bimler et al., 2018), we expect to detect indirect facilitation and the presence of 'native turncoats'. we estimate the effects of neighbors on the fecundity of 20 focal annual plants. Specifically, we statistically fit individual fitness models encompassing both direct and indirect interactions to observed seed sets to infer the strength of species interactions.

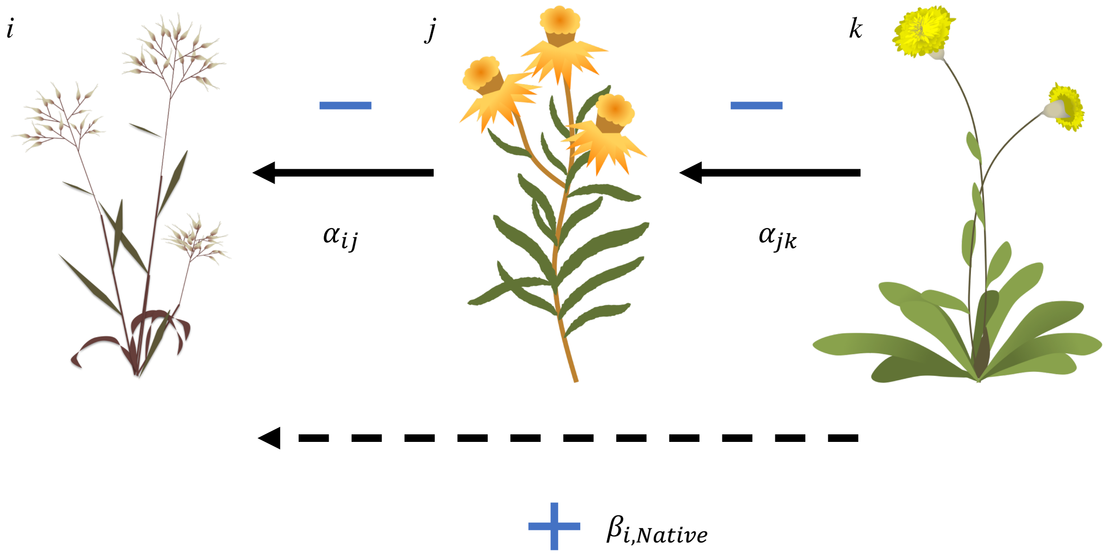

FIGURE 3.1: 'Native turncoats'. Focal species (left) introduced species *Pentaschistis airoides* is negatively affected through direct competition from an intermediate neighbor here depicted as *Waitzia acuminata* (middle). A native species (right) *Podolepis canescens* directly competes with the intermediary neighbor. This competition allows *P. canescens* to indirectly facilitate the focal species as it escapes form direct competition with the intermediary species. Flower illustrations by Xingwen Loy.

Methods

Study System

The annual understory plant communities found in SW Western Australia's York gum-jam woodlands have been identified as one of the world's biodiversity conservation hotspots including both native and introduced species (Myers et al., 2000). This area contains 1.4% of the world's endemic plant species; however, only 10% of the remaining endemic vegetation remains after agricultural clearing (Myers et al., 2000). York gum-jam woodlands characteristically contain a canopy of sparse York gum trees (*Eucalyptus loxophleba* Benth), jam trees (*Acacia acuminata* Benth) and shrubs. Natural species richness in these communities can reach over 25 species per 0.09 m^2 and plant abundances from two to nearly 500 plants within a 0.09 m^2 plot. This system's remarkable diversity of annual native and introduced species provides an ideal system in which to examine the prevalence of 'native turncoats'.

Field Methods

In July 2016, plots were established across Perenjori Reserve, SW Western Australia (29°28′01.3"S 116°12′21.6"E). One-hundred 50 × 50 cm plots were set up around naturally occurring annual plant communities in five blocks each containing 20 individual plots. Each block was separated by at least 100 m from other blocks; within blocks, all plots were at least 0.5 m apart. Plots were established early in the field season (July) and left in place through peak biomass (September) and seed collection (October). Of the 100 plots, 50 plots were left at 100% natural densities (no weeding), 25 plots were thinned to 60% natural density, and 25 plots were thinned to 30%. Thinning in this study did not target any particular species but rather was conducted to bring down the total neighbor density by removing some individuals of all species in a given plot (also performed in Bimler et al., 2018). Note that thinning was done systematically but specific individuals to weed were arbitrarily selected. After thinning, the identity and location of each individual within a plot was recorded using a pantograph at peak-biomass (see Supplemental Material). These maps were then digitized using QGIS an open source geographic information system (GIS) software (QGIS Development Team, 2016). These maps allow for a complete, spatially explicit picture of the neighborhood in which all focal species grew (Fig 3.2); from which we can investigate the relative importance of direct and indirect species interactions on individual fitness.

After mapping all of the plots and when plants were near senescence, seeds were collected from individual focal plants as the fitness metric. It was not possible to collect seed from all focal individuals as some released their seeds before collection. Seed collection varied across plots ranging from 0.0% to 98.5%, with an average of 50% of seeds collected (see Supplemental Material). When feasible, all seeds collected from an individual were counted by hand; if not, seed number was estimated using a micro balance by sub-sampling. These seed data were combined with the individual locations of plants within the plot providing spatially explicit maps of individual fitness across 100 annual plant neighborhoods. These fecundities (seed counts) were then used to infer the strength of species interactions as both direct and indirect neighbors affect the fitness of focal individuals.

Fecundity Model

We aimed to investigate the relative importance of direct and indirect species interactions to individuals. Therefore, we first examined 7.5 cm radius neighborhoods around each focal species to count the number of direct of neighbors. We then applied this same 7.5 cm radius to those direct neighbors to find and count the focal's number of indirect neighbors (Fig 3.2). In this process, direct neighbors and focals were not counted as indirect neighbors. From these neighborhoods, we can calculate how much direct and indirect neighbor abundance alters fecundity of focal individuals. We used neighbor hoods from multiple plots to investigate each focal. The number of observations per focal ranged from 37 to 1158 (Table B.1). We inferred the strength of direct and indirect interactions for individual fitness by predicting fecundity as a function of direct and indirect neighbors. Fecundity equations take the form of:

$$F_{m_i}|\{C\} = r_{b_i}\lambda_i e^{D_{m_i}|\{C\}} e^{H_{m_i}|\{C\}}\,, \tag{3.1}$$

where F_{m_i} is the fecundity of a focal individual m of species i in the presence of a specified community C (Eqn 1). This observed fecundity is a function of the intrinsic fecundity of individuals of species i (λ_i), changes in fecundity associated with growing at a given site (r_{b_i}), and the exponential terms capture the total direct ($D_{m_i}|\{C\}$) and indirect ($H_{m_i}|\{C\}$) effects of all neighboring species in the community (C).

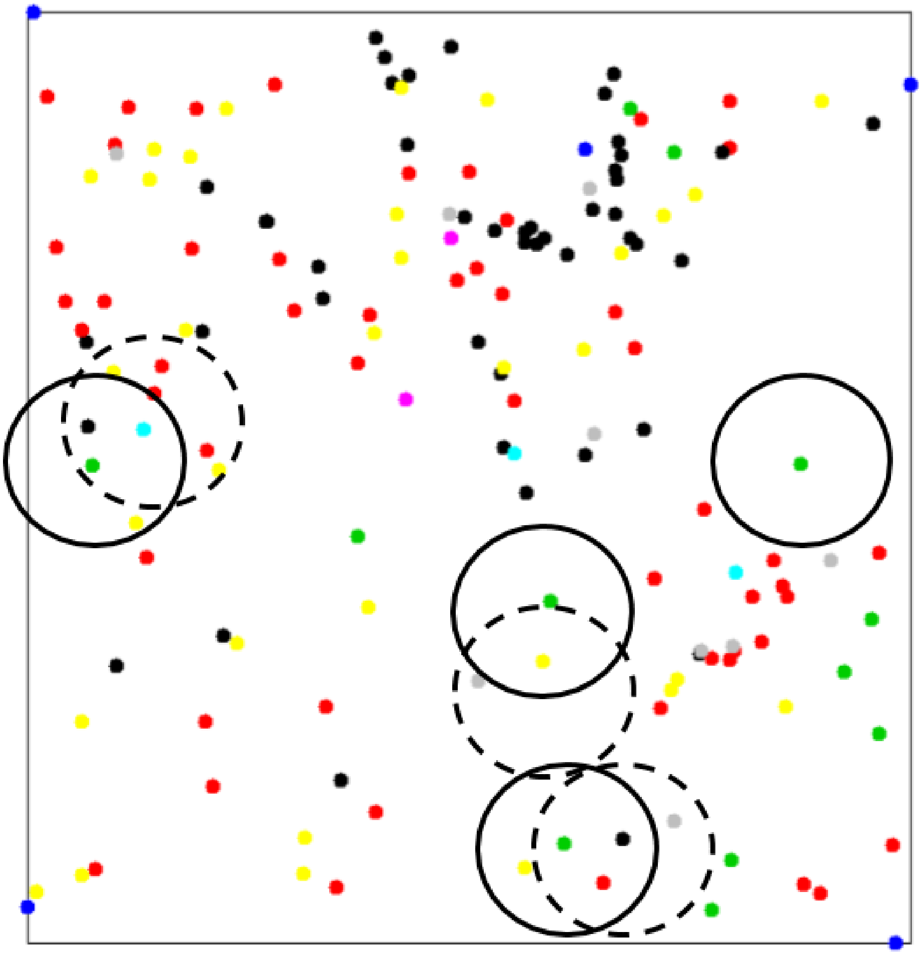

FIGURE 3.2: Example of digitized pantograph map. Each point is an individual plant, with colors representing different species. From these maps we examined different neighborhoods to count the number of direct and indirect neighbors. For example, if we take the green species as the focal species, a direct neighborhood (solid circles) of 7.5 cm radius surround the focal and the number of other individuals in this neighborhood is its direct neighbors. Then the same size neighborhood is placed around those neighbors (dashed circle) to count the number of indirect neighbors. For clarity, of the figure we only highlight a few individuals and neighborhoods but in the analyses this is exhaustive. The four dark blue dots depict the corners of the plot and all focals and neighborhoods were chosen to lie completely within the plot (i.e. not extending outside the sampled area). The map as a whole is a spatially scaled representation of all individual plants in this real plant community. The pantograph was designed to reduce the plot size to a 15 X 15 cm map, a 3:1 reduction.

The total direct effect of neighbors D_{m_i} on focal species is the sum of direct effects of all the surrounding neighbor species S in a given community following the form:

$$D_{m_i}|\{C\} = -\sum_{j=1}^{S} \alpha_{ij} N_j \,, \tag{3.2}$$

where N_j is the abundance of direct neighbors of species j measured based on the 7.5 cm radius neighborhood applied to each focal individuals. α_{ij} is the interaction coefficient measuring the effect of neighbor species j on the focal individual of species i. If $N_i > 0$, then α_{ii} is included in the sum representing conspecific interactions. Importantly these interaction coefficients (α_{ij}) can be positive or negative reflecting competition or facilitation, respectively.

Examining changes in fecundity due solely to the effects of direct neighbors on a focal, while ignoring indirect neighbors, assumes that the effect of direct neighbors is constant regardless of the neighborhood that pair inhabits. However, previous studies have shown this is not always a fair or biologically-appropriate assumption (Mayfield and Stouffer, 2017; Letten and Stouffer, 2019; Kleinhesselink et al., 2019). Given the evidence that indirect neighbors may influence the fecundity of the focal plant, we incorporate the effects of indirect neighbors on the focal species as H_{m_i}:

$$H_{m_i}|\{C\} = -\beta_{i,Conspecific}\mathcal{N}_{Conspecific} - \beta_{i,Introduced}\mathcal{N}_{Introduced} - \beta_{i,Native}\mathcal{N}_{Native} \tag{3.3}$$

Here we classify the indirect interactions into three groups based on the identity of the indirect neighbor: conspecific $\beta_{i,Conspecific}$, introduced $\beta_{i,Introduced}$, and native $\beta_{i,Native}$. Abundance of indirect neighbors is also divided into the same three categories: conspecific $\mathcal{N}_{conspecific}$, introduced $\mathcal{N}_{Introduced}$, and native $\mathcal{N}_{Native}$ based on the identity of the indirect neighbor and regardless of the identity of the direct neighbor. These abundances were counted from the neighborhood measurements described above as the neighborhood surrounding direct neighbors. Note that if there are no direct neighbors ($\sum_{j=1}^{S} N_j = 0$) then there are no indirect neighbors ($\mathcal{N}_{Conspecific}, \mathcal{N}_{Introduced}, \mathcal{N}_{Native} = 0$). $\beta_{i,Conspecific}$ is the interaction coefficient that measures the impact of conspecific indirect interactions, where species i impacts an intermediate species which then impacts the focal individual of species i. Similarly, $\beta_{i,Introduced}$ is where an introduced species impacts an intermediate species which in turn impacts the focal individual of species i. Lastly, $\beta_{i,Native}$ is where a native species impacts an intermediate species which in turn impacts the focal individual of species i. If any of these β interactions are negative this would indicate an indirect facilitative interaction on the focal species. Furthermore, positive interaction coefficients ($\beta > 0$) indicate indirect competition. Here 'native turncoats' would be observed when β_{Native} is negative for an introduced focal species.

Model Inference

We inferred interaction coefficients and intrinsic fecundities by statistically fitting these models to observed fecundities for each focal species separately using a generalized linear mixed-effects model with a log-link function fitted by Laplace approximation (Zuur et al., 2009; Mayfield and Stouffer, 2017). Here, we used abundance of direct and indirect neighbors as fixed factors and blocks as random factors (Zuur et al., 2009). Using the random effect of block to accounts for environmental factors (such as soils phosphorus, soil water, litter, bare space, and canopy cover, see Appendix B for methods and results of environmental variables; Figs B.2 and B.3) which may alter interaction strengths (Bimler et al., 2018) and ensured adequate observations of each focal species and interaction as observations originally at the plot level interactions were pooled. Generalized linear mixed-effects models were fit for each focal species individually in the R statistical environment (R Core Team, 2013; Bates et al., 2015). This species-by-species examination allowed for the estimation of more interactions as many neighbor–focal interactions were often species specific (i.e. individuals from one focal species may tend to interact with the same neighbors species while individuals from a different focal tended to interact with different neighbor species).

Results

Inferred Interactions

We fit the fecundity models to the observed seed production of each of 20 focal individuals to estimate the effects of direct and indirect neighbors on individual fecundity. The number of direct interactions inferred for each focal varied due to different numbers in observed co-occurrences. However, we was able to estimate three types of indirect interactions for all focal species. The mean (± SE) inferred direct interaction coefficient was -0.048 ± 0.117, while the mean indirect interaction coefficient was 0.003 ± 0.0028 (Fig 3.3). In the model, negative interactions ($\alpha_{ij} < 0$) indicate facilitation while positive ($\alpha_{ij} > 0$) indicate competition; therefore, direct interactions were on average facilitative and indirect interactions on average competitive. This dataset included five introduced focal species, with a mean (± SE) inferred direct interaction coefficient of -0.095 ± 0.379, -0.032 ± 0.033 inferred conspecific indirect interaction coefficient, -0.001 ± 0.0002 inferred introduced indirect interaction coefficient, and -0.003 ± 0.006 inferred conspecific native interaction coefficient. One such introduced focal species *Hypochaeris glabra* experienced extreme interactions with both direct and indirect neighbors ranging from -60 to 30 for direct interactions and 0.01 to 0.17 for indirect interactions.

Of the 770 inferred direct and indirect interactions across all species, 347 (45%) were facilitative ($\alpha_{ij} < 0$)). We inferred more direct than indirect interactions (Fig 3.3); however, a large proportion of indirect interactions were faciliative (Fig 3.4). In general, interactions varied in direction and magnitude for each focal species and here we provide a few examples of the ways in which species interacted. We found that one introduced species, *Petrorhagia dubia*, experienced indirect facilitation from native species; that is, this species showed increased seed production in the presence of 'native turncoats'. For native species, native indirect neighbors more often provided benefits than introduced indirect neighbors (Fig 3.4). Nine native focal species (out of 15) experienced indirect facilitation from native neighbors while three native focal species experienced indirect facilitation from introduced neighbors. For example, *Goodenia berardiana* (GOBE) and *Goodenia pusilliflora* (GOPU) —two native species— were both facilitated indirectly by other native species (Fig 3.3). Many focal species (11 out of 20) were facilitated by conspecific indirect neighbors. For example, *Medicago* sp. (MEDI) and *Hypochaeris glabra* (HYPO)—two introduced species—and *Podolepis lessonii* (POLE) and *Velleia cycnopotamica* (VECY)—two native focal species— had facilitative interactions with their respective conspecific indirect neighbors.

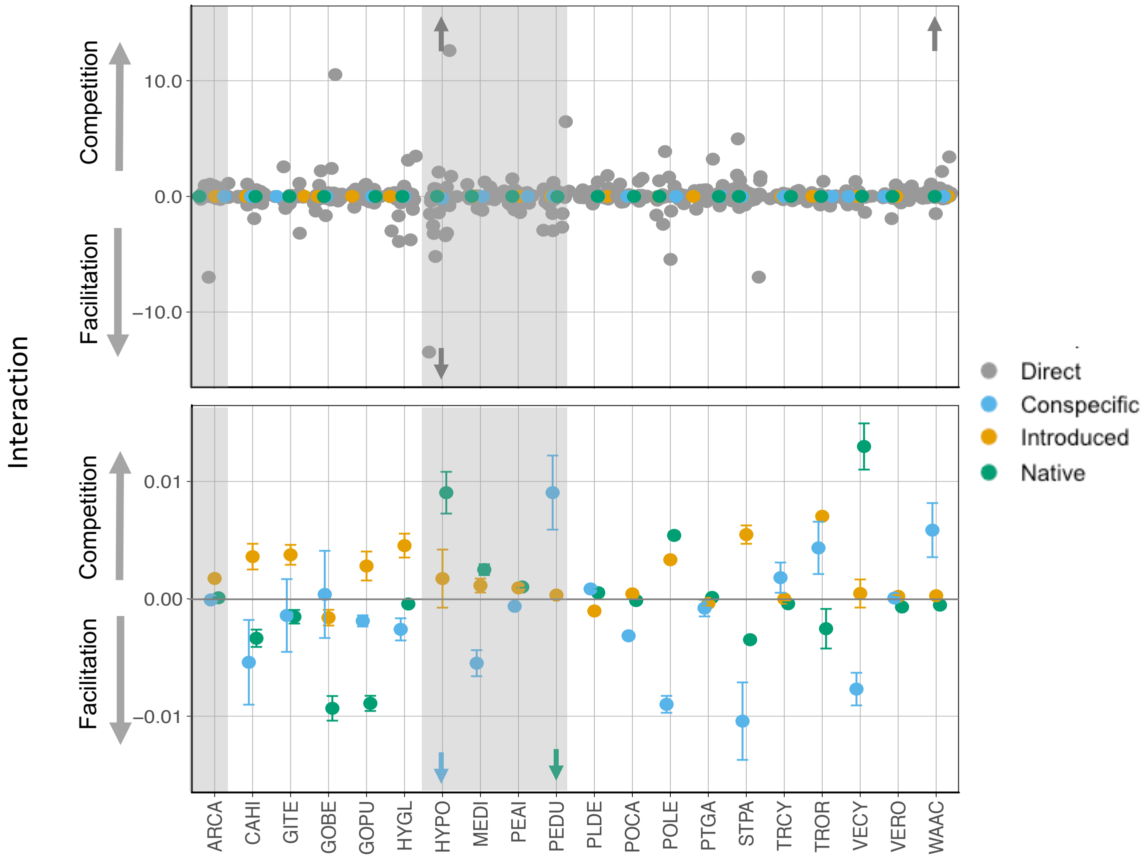

FIGURE 3.3: Distribution of estimated interaction coefficients across focal species. According to the fecundity model, interaction coefficients greater than zero indicate competition while those below zero indicate facilitation. 'Native turncoats' are shown as faciliative interactions by native indirect neighbors on introduced focals. Introduced focal species are shown in the shaded regions, while arrows indicate interaction coefficients beyond the axis limits. Top: All focal species and all interaction types (both direct and indirect). Direct interactions are estimated from the count of direct neighbors while indirect interactions refer to the count of the three categories of indirect neighbors. Indirect interactions were estimated as categories: introduced, where the indirect neighbor is an introduced species; native, where the indirect neighbor is native; and conspecific where the indirect neighbor is the same species as the focal species. Bottom: Distribution of estimated indirect interactions across all focal species. These are the same as the blue, yellow and green points in the top panel but spread out for clarity. Error bars are ±1 SE. See Table B.1 for species names associated with each species code on the x-axis.

Predicted Fecundity

Variation in magnitude and direction of interactions generated a range of responses in predicted fecundity; therefore, we only highlight a few examples here. PEDU—the only introduced species to evidently benefit from from 'native turncoats'— showed high inferred intrinsic fecundity and increasing predicted fecundity with increasing abundance of conspecific direct neighbors (Fig 3.5 E and F). In this case, indirect native neighbors increased PEDU's predicted fecundity, doubling it from what is predicted under direct conspecific interactions alone. While interactions with conspecific indirect neighbors decreased this species' predicted fecundity and interactions with introduced indirect neighbors did not alter the fecundity compared to conspecific direct neighbors (Fig 3.5). These results suggest that individuals of PEDU

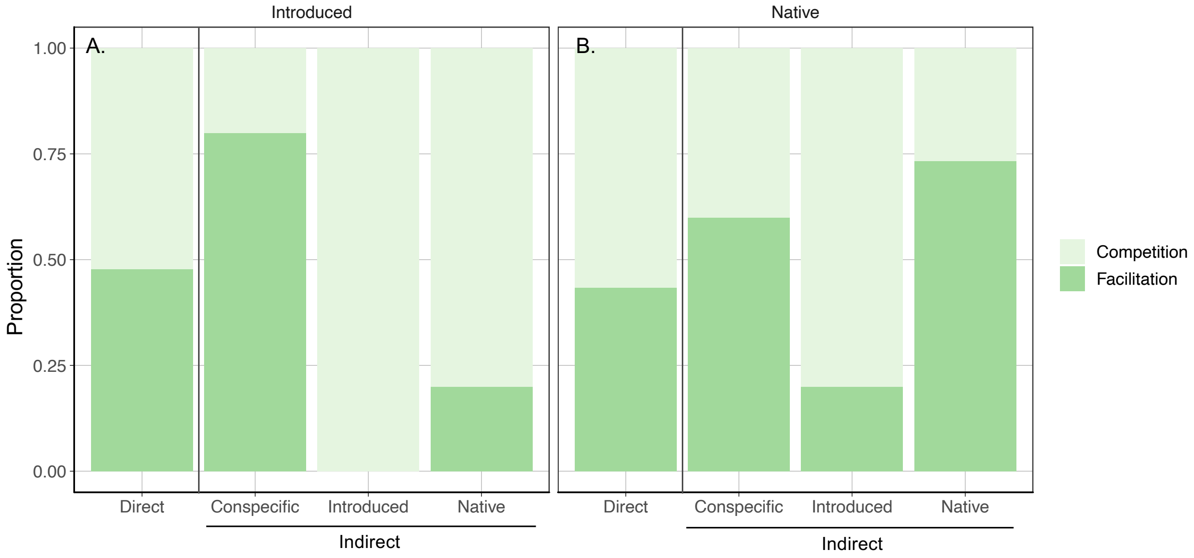

FIGURE 3.4: Proportion of direct and indirect interactions which were facilitative or competitive. A: proportion of interactions which were competitive or facilitative as experienced by introduced focal species. B: proportion of interactions which were competitive or facilitative as experienced by native focal species. 'Native turncoats' can be seen through the facilitative interactions of indirect native species on introduced focal species (A); present in one of the five focal individuals. Direct interactions are estimated from the abundance of direct neighbors and includes more estimates than indirect interactions. Indirect interactions were estimated as categories: introduced, where the indirect neighbor is an introduced species; native, where the indirect neighbor is native; and conspecific where the indirect neighbor is the same species as the focal species.

produce more seeds when living in a neighborhood of native species with a sparse density of conspecifics.

The opposite situation can be seen for *Arctotheca calendula* (ARCA), also an introduced focal species. The predicted fecundity of ARCA showed a decline in fecundity with increasing conspecific neighbor density and this decline increased in the presence of introduced indirect neighbors (Fig 3.5). 'Native turncoats' were not present in this example. Instead native indirect neighbors had a small competitive effect on ARCA lowering its predicted fecundity (Fig 3.5). On the other hand, conspecific indirect neighbors led to an increase in predicted fecundity suggesting that ARCA living in a dense monculture produces more seeds than those living in sparse monoculture and/or diverse patches. Another example, MEDI—an introduced species— exhibits decreasing fecundity as conspecific direct neighbor density increases, but with the addition of conspecific indirect neighbors this fecundity is higher. Native and introduced indirect neighbors did not alter fecundity. These represent a few examples of how focal species' responded to both direct and indirect neighbors and how these interactions translate into fecundity of the focal species.

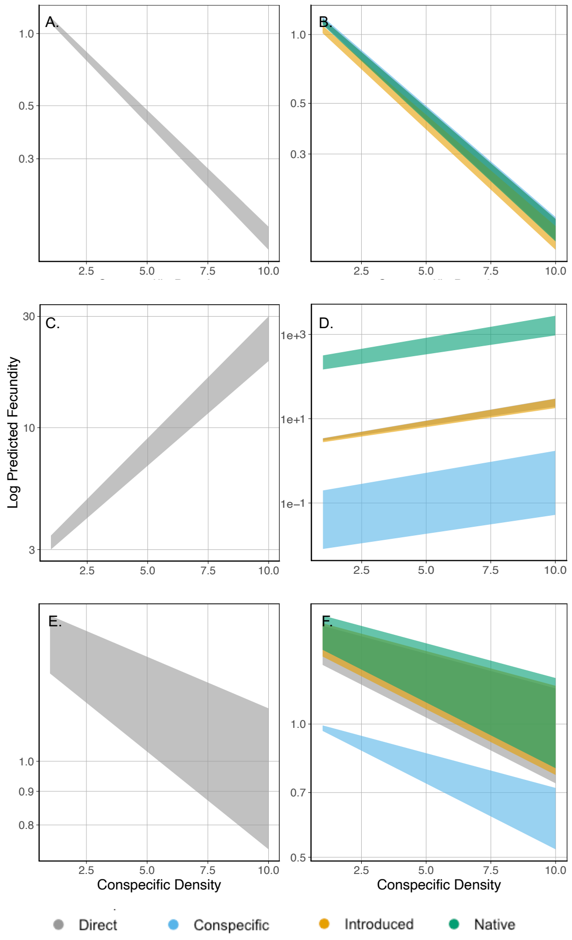

FIGURE 3.5: Realized effect of indirect neighbors on predicted fecundity of multiple introduced focal species predicted across a range from one to ten conspecific direct neighbors and the mean of total indirect neighbors (mean of conspecific + native + introduced) for the density of each type. Each row shows the predicted fecundity of an individual focal species while left panels show the effect of direct conspecific neighbors (gray color) on this focal's fecundity while the right panels show indirect interaction types (conspecific indirect interactions in blue; native in green; and introduced in orange) and direct interactions. Fecundity is shown on a log scale. Each line represents plus, minus one standard error of the mean estimate (±SE). A: *A. calendula* (ARCA) shows decreasing fecundity as conspecific direct neighbor density increases. B: There is little effect of conspecific or native indirect neighbors and a competitive effect of introduced indirect neighbors resulting in a lower fecundity. C: *P. dubia* (PEDU) displays increasing fecundity with increasing conspecific neighbor density. D: Indirect introduced neighbors do not alter *P. dubia*'s predicted fecundity (directly on top of the gray ribbon) while native indirect neighbors increase its fecundity and conspecific indirect neighbors decrease it compared to only direct interactions. E: *Medicago* sp. (MEDI) exhibits decreasing fecundity as conspecific direct neighbor density increases. F: The addition of conspecific indirect neighbors decreases fecundity further. Native and introduced indirect neighbors did not alter fecundity (are pictured directly on top of the gray ribbon).

Discussion

Results identify the presence of 'native turncoats': indirect facilitation of an introduced species by a native species (Northfield et al., 2015). To our knowledge, this is the first data-informed detection of these types of interactions in natural communities. While only one out of the five introduced focal species showed a benefit of ‘native turncoats’, these interactions had measurable effects on the fitness outcomes (fecundity) of the introduced species in question (*Petrorhagia dubia*). These results show that indirect interactions should not be simply ignored as there are always more indirect than direct interactions in diverse systems making the relative importance of indirect interactions is greater even when they are small in magnitude.

Despite invasion ecology tending to focus predominantly on competitive interactions when examining both the impact of introduced species on native communities and resistance of native communities to introduced species, we found many examples of facilitation in this study with 45% of both direct and indirect interactions being facilitative (Fig 3.4). While in low proportion (20%), we found examples of introduced species indirectly facilitating native species (Fig 3.4). More often, we found native neighbors indirectly facilitating native focal species (Fig 3.4). There are many examples in the literature of introduced species that involve facilitation between introduced species, termed ‘invasional meltdown’ (Simberloff and Von Holle, 1999). For example, Elton (Elton, 1958) described how Argentine ants (a neotropical ant, *Linepithema humile*) remove some of the natural enemies of the Asian scale insects (*Aonidiella aurantii*) in California citrus orchards. Argentine ants therefore indirectly facilitate citrus by removing the scale insects which would otherwise eat the plant. This example illustrates that facilitation among species does not require co-evolutionary history nor does it require direct interactions (Simberloff and Von Holle, 1999). In this study, we found no support for indirect ‘invasional meltdown’ between species as indirect effects of introduced neighbors did not facilitate introduced focal species (Figs 3.3 and 3.4). However, some introduced focal species were facilitated directly by introduced neighbors and individuals of their own species. For example, the predicted fecundity of *Petrorhagia dubia*’s (an introduced species) increased with increased representation of direct conspecifics in neighborhoods which may be an example of ‘invasional meltdown’. On the other hand, *Arctotheca calendula* was hindered by direct interactions with conspecifics but facilitated by indirect conspecific neighbors. While ‘invasional meltdown’ might be present in these communities, we look to Simberloff and Von Holle’s (Simberloff and Von Holle, 1999) to highlight that facilitation of introduced species need not be generated by co-evolution including indirect facilitation among native and introduced species through ‘native turncoats’.

The previous paradigm of ‘biotic resistance’ relies on the idea that direct competitive interactions explain why some introduced species survive and spread and why the others fail (Elton, 1927). This theory proposes that some communities can protect themselves from introductions by out-competing incoming species, and hinges on the idea that in highly diverse resident communities, all the resources are spoken for, leaving no room for the introduced species (e.g. (Tilman, 1997; Stachowicz et al., 1999; Marraffini and Geller, 2015). Yet as the diversity of a community increases so does that number of indirect interactions, including facilitative ones which may allow introduced species to establish. In the diverse system, we measured, many facilitative interactions were found, both direct and indirect, with no overarching support for the idea of ‘biotic resistance’ as native residents facilitated introduced species.

In this study of a highly diverse annual plant system, five introduced species have been established perhaps in part due to positive indirect interactions with resident species. These facilitative interactions can have large impacts on seed production (Fig 3.5) which is the first step to a successful introduction. While originally framed as a type of population-level phenomenon, we investigated 'native turncoats' on an individual level as the net facilitative impact of native indirect neighbors on the fecundity of individuals of introduced species (Fig 3.1). Similar to other coexistence studies, here we have investigated interaction effects on a single life stage (adults) and a single vital rate (fecundity). Recent reviews of competitive interactions in annual plants highlight that this intense study of the performance of individual plants have told us little about how such competitive effects translate to effects on whole populations (Aschehoug et al., 2016). Successful introductions and subsequent population-level coexistence depend on multiple life stages and vital rates (Broekman et al., 2019), as they unequally contribute to per capita population growth (De Kroon et al., 2000). Fundamentally, invasion success relates to averaged population growth over time spanning the introduction, spread, and success of species and is impact by a wide range of factors including competition and facilitation. The effects of one life stage may, for instance, be offset by another (Moll and Brown, 2008; Visser et al., 2016). While we acknowledged the limitations of this and similar studies as increased fecundity of an introduced species does not guarantee successful invasion, it is likely to increase the probability of success and therefore remains an important metric to study.

Here we demonstrate the presence of 'native turncoats' by measuring the indirect facilitation of one introduced annual plant species in this study. This study system included five introduced annual plant species, four of which were forbs and one grass, only one of which supported 'native turncoats' (*Petrorhagia dubia*, a forb). For better or for worse, this limits the generality of our conclusions. Though we have provided evidence that 'native turncoats' do exist, this study was not broad enough to speak to the commonality of this phenomenon. This study was also unable to determine which native species provided the most indirect facilitation due to data limitations, instead, we quantified how native indirect neighbors collectively affected fecundity. Though lumping together of neighbors is common across the literature (Morales-Castilla et al., 2015; Mayfield and Stouffer, 2017), doing so limits species-specific inferences about which native species may be more responsible for indirect facilitation seen in this study. To combat such limitations in the future, we suggest studying fewer species with a structured experimental setup to explicitly test for the presence of 'native turncoats': with fewer focal and neighbor species as well as more observations per focal and indirect neighbor interactions one could feasibly measure specific interactions. For example, one degree of specificity is separating out indirect neighbors to determine if specific native species have more effects than others. Another is investigating the role of the intermediate species which could modify indirect effects. Both of these avenues would require substantially more data than we had on hand. One rule of thumb suggests ten or more data points per model term to avoid model overfitting (Burnham and Anderson, 2002b; Mayfield and Stouffer, 2017). This system of 20 focal species each with 17-25 direct neighbors, each with multiple neighbors leads to more than one hundred model parameters requiring thousands of observations per focal species. Despite these limitations, this study shows that we may need to expand our view of possible mechanisms of invasion if we are to gain further insights and reach generalizations about biological invasions. While 'native turncoats' likely only tell part of the story, the inclusion of indirect interactions in invasion ecology may help illuminate general patterns in spite of the 'invasion paradox'.

Acknowledgments

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Chapter 4

Interactions and life-history trade-offs govern persistence in space-limited benthic communities

Abstract

The struggle for coexistence arises when co-occurring organisms compete for limiting resources. From forests to corals, lichens, and sponges, one such resource is space. In many space-limited communities, hierarchical organization patterns are the norm, where species A beats B, species B beats C, and hence A beats C can be observed. As a result of these hierarchical organization patterns, it is assumed that the coexistence of these communities is maintained by non-equilibrium forces–predation or physical disturbance—in order to prevent monopolization by one or few competitive dominants. On the other hand, in equilibrium communities we expect niche differences to stabilize coexistence. We aimed to explore mechanisms of coexistence in these space-limited communities by quantifying interactions among functional groups to determine if competitive hierarchies are the dominant organization. We examined benthic marine invertebrates communities and quantified changes in cover of abundant taxa over four months. We then used these changes in cover to infer the population dynamics of co-occurring functional groups finding both competitive and facilitative interactions. We used pairwise interaction coefficients to rank functional groups by competitive ability finding the colonial-soft-encrusting group to be dominant in these assemblages. We also measured life-history trade-offs with the general trend that groups with weaker competitive interactions or experienced more competition had higher recruitment levels. Additionally, in pairwise simulations using inferred parameters, all groups persisted and none were driven extinct. Taken together, we conclude that coexistence in this space-limited community is maintained by multiple, non-mutually exclusive mechanisms: trait differences acting as an equalizing mechanism, life-history trade-offs, and facilitation across a gradient of neighbor density. Disentangling the effects of these interactions and in turn patterns of coexistence represents an important step in understanding the maintenance of diversity in diverse, space-limited systems.

Keywords: Space-limited communities, Coexistence, Competition-colonization trade-offs, Facilitation

Introduction

The factors enabling the coexistence of species are an ecological puzzle, the understanding of which has implications for endangered species conservation (DeCesare et al., 2010), the control of biological invasions (MacDougall et al., 2009), and predicting global climate change impacts (Chu et al., 2016). Theory predicts that the species which can best compete for limiting resources will drive competitively inferior species extinct (Chesson, 2000b; HilleRisLambers et al., 2012). However, a community of species can stably co-occur, via multiple coexistence mechanisms, over long periods of time if members of the community are buffered against extinction (HilleRisLambers et al., 2012). Even slight differences in morphology, physiology, or life-history traits among similar species can reduce competitions by partitioning shared resources in type, time, and/or space (Dudgeon et al., 1999). Yet many generalist species that can coexist have broadly overlapping patterns of resource use (Dudgeon et al., 1999; Connell, 1978), leading to the search for mechanisms that allow many groups to persist in natural communities.

One shared resource, space, is the subject of competition for many organisms and ecosystems including corals (Lirman, 2001), lichen (Crowley et al., 2005), vascular plants (Matlack, 2002), grasslands (Tilman, 1994), sponges (Sebens, 1986), and more (see (Amarasekare, 2003) for review). In many space-limited communities, interactions between species follow competitive hierarchies leading to monopolization by a competitive dominant (Quinn, 1982). As a result of these hierarchical organization patterns, it is assumed that the coexistence of these non-equilibrium communities is maintained by predation or physical disturbance that prevents monopolization by one or few competitive dominants (Paine, 1966, 1974b; Dayton, 1971; Connell, 1978). For example, hierarchical competition is seen in mussel-barnacle-algal communities of the mid-upper rocky intertidal zone (Paine, 1966, 1969; Dayton, 1971). Intertidal mussels can displace other large sessile species (e.g. seaweed and barnacles), thereby reducing the diversity of primary space holders but predation by seastars keeps the mussel population in check allowing for coexistence of mussel-barnacle-algal communities (Paine, 1966, 1969). This outside force, predation, disproportionately affects the dominant species preventing its monopolization of resources and allowing inferior competitors to remain in the community.

Life-history trade-offs can provide a mechanism for coexistence in hierarchical systems. Whereby superior competitors can have the following characteristics: lower fecundity, recruitment or dispersal-limitations, or lack the ability to quickly exploit recently disturbed or early successional habitats (Amarasekare, 2003). On the other hand, inferior competitors have higher fecundity, recruitment ability, or long dispersal ranges— allowing them to exploit resource-rich or early successional habitats and can disperse offspring before superior competitors arrive (Bolker and Pacala, 1999). Competition-colonization trade-offs can commonly be seen during succession where early colonizers are quickly outcompeted by later successional species (Sebens, 1986; Tilman, 1994). Alternatively, if space-limited communities coexist at equilibrium, diversity may be maintained by niche differences whereby species separate their resource use, for example, coexisting plants acquiring resources from different soil depths (Chesson, 2000b;

Levine and HilleRisLambers, 2009; Letten et al., 2017). Niche differences work to stabilize competitor dynamics by giving species higher per capita population growth rates when rare compared to when at high density and when these effects are greater than competitive abilities differences species can coexist (Chesson, 2000b; Levine and HilleRisLambers, 2009).

Additionally, previous conceptual theories and empirical approaches in space-limited systems have highlighted the role of facilitation in these communities, finding that by incorporating facilitation into our understanding the spatial extent of the realized niche of a species may be larger than the fundamental niche (Bruno et al., 2003b; Hart and Marshall, 2013). In the current study, we use marine benthic communities to understand what or which mechanisms allow coexistence in space-limited systems. We quantify interactions among functional groups in a space-limited community to determine if competitive hierarchies are the dominant organization structures. Marine benthic communities are generally thought to be space-limited and organized by an approximate hierarchy of competitive abilities (Quinn, 1982); however, these studies are often conducted in simple communities of few species. Unlike these studies, we examine the dynamics of diverse communities with up to seven functional groups.

Benthic marine invertebrate communities are space-limited, living on hard substrates such as rocky reefs as well as man-made structures of marinas (Sutherland, 1981; Stachowicz et al., 1999). These communities have previously been considered fundamentally simple and contain easily observable interactions (Buss, 1980; Hart et al., 2012). However, this impression of simplicity has often resulted in simple categorical assessments of competition and coexistence with a focus on winners and losers of interactions among individuals and the assumption of competition for a single limiting resource (space) via simple mechanisms (overgrowth) (e.g. Buss, 1980; Quinn, 1982; Jackson, 1979; Sellheim et al., 2010). Sessile species—those that live largely attached to a hard substrate— that make up these benthic marine invertebrate communities are a mixture of tunicates, bryozoans, mussels, hydroids, sponges, and other invertebrate taxa (Ruiz et al., 2000). Benthic marine invertebrates have different growth forms and space requirements which should allow them to differentiate along a niche axis, limit resource-use overlap, and therefore, weaken the overall strength of interspecific competition (Hart and Marshall, 2009). For example, colonial ascidians are thought to be strong interspecific competitors (Russ, 1982; Keough, 1984) and can grow almost unimpeded growing on top of heterospecific competitors but can be limited for space by conspecifics (Hart and Marshall, 2009). On the other hand, bryozoans are considered weak competitors exhibiting weedy traits, able to exploit space early but are later outcompeted (Russ, 1982; Keough, 1984; Buss, 1990; Hart and Marshall, 2009). Despite these generalities, competitive hierarchies in marine sessile organisms are often qualified as win/loss outcome of overgrowth (one organism on top of another) (Barnes and Neutel, 2016) or in very simplified communities (Hart et al., 2012). Therefore, we intend to quantify interactions among different functional groups to explore the possibility of competitive hierarchies and ultimately what drives coexistence in these space-limited benthic marine invertebrate communities.

We experimentally tracked changes in percent cover over time to quantify interactions among functional groups. We use a phenomenological approach to population dynamics which does not allow for the understanding of the exact mechanisms of competition (i.e. for space, interference competition, or food competition) but rather measures the responses to the aggregate effects of competition for multiple resources. We predict that groups will both compete and facilitate with each other yet follow a competitive hierarchy with a dominant group. Specifically, we predict that colonial ascidians (which make up the functional group colonial soft encrusting) will be a strong competitor given their ability to overgrow many neighbors (Russ, 1982; Keough, 1984; Hart and Marshall, 2009) and colonial calcified bryozoans (colonial calcified encrusting) are a more weedy group and weaker competitors (Russ, 1982; Keough, 1984; Buss, 1990; Hart and Marshall, 2009). We also predict facilitation interactions among groups, for instance, solitary calcified organisms such as mussels may provide additional hard substrate for colonial ascidians or other encrusting organisms (Sellheim et al., 2010). However, we expect to find variability of the interactions among these groups as the same pair may facilitate or compete under different circumstances. Colonization rates and life-history trade-offs will allow the less competitive functional groups to persist even in the presence of a competitive dominant. We also expect that indirect interactions may be additionally responsible for coexistence outcomes whereby pairs of functional groups cannot coexist but in triplicate or larger those groups can persist.

Methods

Field Methods

To quantify interactions in fouling communities, organisms living on hard substrates typically boats and marinas, we used data collected in the marine fouling community of Monterey Harbor central California, USA in April through October 2012. Adult individuals of 16 species were collected in June 2012 from Monterey Harbor, Monterey, CA (see Marraffini and Geller, 2015, for species list) and attached to PVC tiles (20x20cm) at varying richness levels (1-8 species) (Marraffini and Geller, 2015). All tiles hung horizontally 0.2—0.4 m below floating docks. Tiles were placed facing down to encourage invertebrate recruitment, as many larvae are photonegative (Glasby, 2001; Glasby and Connell, 2001). Communities were photographed in-situ using a Panasonic Lumix TS20 waterproof camera mounted on a 40 cm rod to capture the entire tile in a single frame. Photographs were taken every two weeks for four months yielding six observations per tile. See Marraffini and Geller 2015 for additional field methods.

Empirical Data

From field photographs, percent cover of organisms was calculated using a system of random points overlaid on each photograph (PhotoGridB (Bird, 2002)). These photos were edited using Adobe PHOTOSHOP CS3 to remove background and adjust exposure as needed. Percentage cover of the community was estimated using PHOTOGRID v. 1.0 beta (Bird, 2002), where each photo received 50 points generated in a fully random fashion (Foster et al., 1991). Organisms

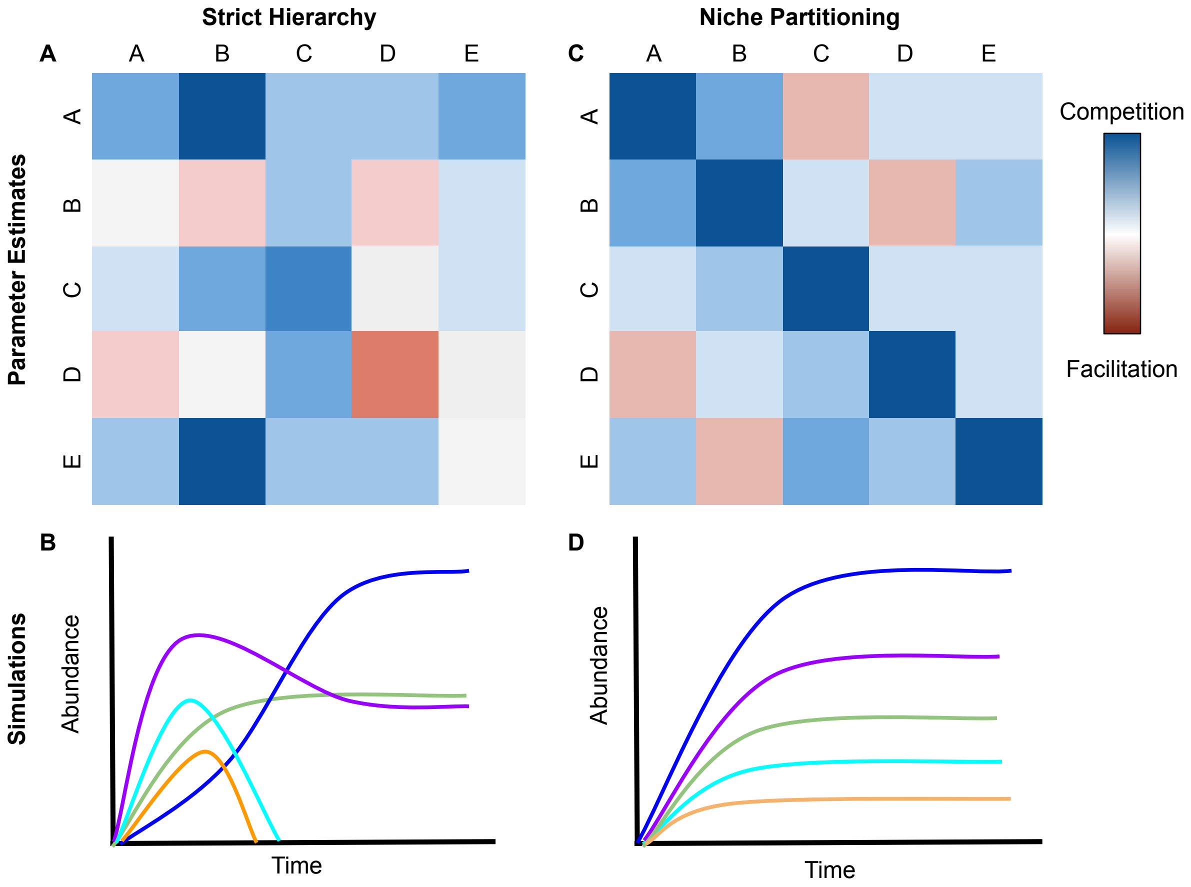

FIGURE 4.1: Hypothetical results under two scenarios of coexistence mechanisms. A) If the communities have a strict competitive hierarchy groups can be ranked by competitive ability. Competitive rank, based on pairwise interactions, is derived by subtracting the competitive effects (sum of each row) from the responses of all other groups in the community (sum of each column), then taking the absolute value. In this example, groups are ranked A>B>C>D>E, where the difference between the column and row sums is largest for group A and smallest for group E. B) Lower competitive ranked groups may go extinct if they can not effectively compete or recruit into the community. However, inferior groups can persist in the community by multiple mechanisms including competition-colonization trade-offs, whereby early colonizers can quickly disperse into new spaces but is out competed by stronger competitor(s) which arrive later. C) If communities are dominated by niche partitioning, pairwise group interactions will show a pattern of stronger competitive intra-specific interactions compared to inter-specific interactions as groups limit themselves more than others. D) In these communities, groups will reach equilibrium with different relative abundances based on their carrying capacity for their niche. In both scenarios, pairwise group interactions may be competitive or facilitative and under the right conditions all groups may persist in the community simulations.

under each point were identified to the lowest taxonomic level through morphological identification, and confirmed using genetic methods (when morphological identifications were not feasible) prior to analyses (Marraffini and Geller, 2015).

Organisms were then classified into functional groups according to their growth form (colonial or solitary), body type (calcified or soft), and dimensionality (encrusting, upright, or runner). We observed seven groups of the possible 12 combinations of these three functional types (Table 4.1 for each label and species there in). While some of our species are known to take on multiple growth forms, We classified them based on the most common form seen in our experiment. For example, *Watersipora subtorquata* is known to form large, structurally complex lettuce-like heads (personal observation, (Sellheim et al., 2010)); however, in our study this species did not form these structures and rather remained encrusting on the surface of the experimental tiles. In total, we examined 277 assemblage tiles over the six time points resulting in 8050 observations of our seven focal functional groups.

TABLE 4.1: Functional groups recorded in assemblages and used as focal and neighbor function groups. Group name, genus and species names, and higher classifications of family and phyla. Two morphotaxa remain as unidentified to the genus level.

Functional group	Species Recorded	Family	Phyla
Solitary Soft Upright	*Ascidia ceratodes*	Ascidiidae	Chordata
	Ciona savignyi	Cionidae	Chordata
	Metridium senile	Metridiidae	Cnidaria
	Corynactis californica	Corallimorphidae	Cnidaria
Solitary Calcified Upright	*Mytilus californianus*	Mytilidae	Mullusca
	Mytilus galloprovincialis	Mytilidae	Mullusca
	Balanus crenatus	Balanidae	Anthropoda
Solitary Calcified Runner	*Spirorbis spp.*	Serpulidae	Annelida
Solitary Soft Runner	*Eudistylia polymorpha*	Sabellidae	Annelida
Colonial Soft Encrusting	*Diplosoma listerianum*	Didemnidae	Chordata
	Distaplia occidentalis	Holozoidae	Chordata
	Botryllodies violaceus	Styelidae	Chordata
	Botryllus schlosseri	Styelidae	Chordata
	Colonial tunicate	-	Chordata
Colonial Calcified Encrusting	*Watersipora subtorquata*	Watersiporidae	Bryozoa
Colonial Soft Upright	*Barentsia ramosa*	Barentsiidae	Entoprocta
	Hydroid	-	Entoprocta

Population-Dynamics Model

To quantify functional group dynamics, we developed a discrete-time population-dynamics model that predicts changes in organismal percent cover as a combination of density-independent and density-dependent changes (Rees et al., 1996; Adler et al., 2012; Martorell and Freckleton, 2014). Specifically, we estimated percent cover $N_{i,t+1}$ of a focal functional group i in a future time point $t+1$ as a function of the prior time point's percent cover $N_{i,t}$ with a modified Ricker model (Ricker, 1954; Hart et al., 2012; Hart and Marshall, 2013) and that takes the general form:

$$N_{i,t+1} = Q_i + N_{i,t}\, e^{G_i|\{C_t\}} \tag{4.1}$$

where Q_i represents density-independent increase in percent cover (influx) and G_i represents density-dependent increase in percent cover. Density-independent percent cover, Q_i, may be attributed to recruitment of new larva into the plot (Eqn 4.2). Note that this Q_i term is not influenced by previous percent cover. Mathematically this helps us account for observations of a functional group that were unobserved in the previous time point, something that occurred in 7% of our observations.

$$Q_i = \frac{0.5}{1 + e^{-q_i}} \tag{4.2}$$

Here q_i is inferred from our model fitting and transformed into Q_i, density-independent increase in percent cover (influx) as organisms recruit into the community.

The model component $e^{G_i|\{C_t\}}$ captures density-dependent changes in percent cover since it is multiplied by previous percent cover; these changes can be driven, for example, by growth or mortality.

$$G_i|\{C\} = \lambda_i - \sum_{j=1}^{c} \alpha_{ij} N_{j,t}\,, \tag{4.3}$$

Density-dependent growth (G_i), is the logarithmic intrinsic growth rate of the focal functional group (λ_i) minus the sum of pairwise group interactions with neighboring groups ($\alpha_{ij} N_{j,t}$). Where $N_{j,t}$ is the abundance of focal group j, α_{ij} is the effect of functional group j on the focal functional group i, this is summed across all groups in C community surrounding that focal functional group. If $N_i > 0$, then α_{ii} is included in the sum representing intra-group interactions. Importantly these interactions (α_{ij}) can be positive or negative reflecting competition or facilitation, respectively.

Model Inference

We fit our population dynamics model to the percent cover data in order to infer the model parameters. In this data set, there are 49 potential interaction pairs (seven focal functional groups × seven neighboring functional groups) and observations of each interacting pairs ranged from 7 to 730 with a mean of 204 observations. All focal functional groups were fit simultaneously. We allowed the effects of neighbors to vary for each focal functional group through a random effect resulting in an 'average functional-group' component and a 'group-specific' effect. This model formulation us to infer functional group specific recruitment, intrinsic growth, and neighbor interactions with fewer parameters than if these were included as main effects. This pooling through a random effect also helps account for over-dispersion and unequal observations of some interactions (McElreath, 2012, 2016). In practice, recruitment Q_i of a functional group i is given by a combination of common (population level fixed effect, q_{common}) and functional group-specific deviations (Δq_i) of the form: $(q_i = q_{common} + \Delta q_i)$. Similarly, we parameterized intrinsic growth (λ_i) and density-dependent change $G_i|\{C\}$ of a functional group i such that it contained both the common and functional group-specific effects ($\lambda_i = \lambda_{common} + \Delta\lambda_i$, and $\alpha_{common,j} + \Delta\alpha_{ij}$, respectively).

We fit this model using Bayesian inference with a hierarchical model with Hamilton Markov Chain Monte Carlo (HMCMC), weakly informative priors, and a zero-inflated beta distribution for the response variable (Bürkner, 2017). We used a beta distribution to generate predicted percent cover as it is ideal for continuous populations and allows for a flexible shape (U-shaped, L-shaped, etc) (Wright et al., 2017; Damgaard and Irvine, 2019) and also allows us to a address the treatment of zero percent cover values, common issue of percent cover datasets (Wright et al., 2017; Damgaard and Irvine, 2019). This distribution is also flexible in shape and can handle percent cover data which can be skewed in one of multiple directions (Damgaard and Irvine, 2019).

We performed sampling to determine the posterior distributions of model parameters through the function "brm" from the package "brms" (Bürkner, 2017) in the statistical program R (version 3.4.2) (R Core Team, 2013). We ran three chains with a warm-up of 1000 iterations and 4000 sampling iterations each, and this produced a final combined posterior of 9000 MCMC samples for each model. We determined that parameters converged when trace plots were well mixed and stationary, and the Gelman-Rubin convergence diagnostic was close to one (Gelman and Rubin, 1992; Brooks and Gelman, 1998).

We defined the varying effects of each focal functional group that correspond to deviations from the grand mean (Δ parameters), using a non-centered parametrization of a multivariate normal distribution (Gut, 2009b) with a mean (σ) and covariance matrix (ρ) between the varying effects for each functional group (Eqn 6). We used weakly informative priors of half Cauchy for the mean and LKJcorr(1) for the covariance matrix (Eqn 7-8) (McElreath, 2016). In our model, this prior is skeptical of extreme correlations between the functional group as we allow each group to respond to treatments individually. See supplemental material for additional details on model fitting and prior specification.

Simulations

Inferred parameters were also used to simulate functional group abundances over 10 time steps (Eqn 4.1), exploring mono-culture, pairwise, and an all seven-group poly-culture. One time step represents two-weeks to be on the same time scale as the observations, resulting in a total of a 20 week simulation. We used median inferred values of all parameters. Monoculture simulations varied starting population sizes (ten uniform values between 0 and 1) of each functional group to explore different scenarios. While in pairwise and 7-species polyculture simulations started with initial population sizes set to zero.

Ranking and Trade-offs

We used inferred interaction coefficients from the the above population dynamics model to rank functional group in terms of their competitive ability in pairwise interactions. Ranking (R) is generated by summing the columns of the functional group interaction matrix (community response, $\sum \alpha_{ij}$) and subtracting the sum of the rows (community effects, $\sum \alpha_{ji}$), then taking the absolute value (Roxburgh and Wilson, 2000; Mouquet et al., 2004; Haddad et al., 2008; Carrara et al., 2015). Such that an individual functional group i has the ranking R_i given by:

$$R_i = |\sum_j (\alpha_{ij} - \alpha_{ji})| \tag{4.4}$$

To examine colonization-competition trade-offs, we examined the relationship between inferred recruitment parameters and competition. Similarly to rankings, we measured competition in using two metrics: the effect of a functional group as the column sums of our inferred pairwise interaction matrix (community response, α_{ij}) and the effect on a functional group as the row sums of our inferred pairwise interaction matrix (community effects, α_{ji}). Both metrics were compared to inferred recruitment for that functional group (Q_i). This was examined for 1000 draws of the posterior.

Results

Parameter estimates

Median inferred density-dependent growth rates varied between with solitary calcified upright group having the lowest and colonial soft encrusting having the highest (Fig 4.2 B). Similarly, colonial soft encrusting group had the highest median inferred density-independent recruitment rate at 0.105 while solitary calcified runner group had the lowest at 0.06 (Fig 4.2 A). High density-dependent growth rates of colonial soft encrusting group may also be related to their high levels of recruitment, with juveniles quickly increasing in size compared to large adults who's growth may be impeded by interactions with neighbors. The solitary calcified runner functional group, made up *Spirobis*, showed the widest variability in density-dependent growth rate and lowest recruitment rates, which may be due to its generally small size making it easily missed in photographs. In general, there were not large patterns in inferred parameters based on the three functional traits examined. Apart from colonial soft encrusting group, functional groups regardless of functional traits examined showed similar order of magnitude in inferred density dependent growth (Fig 4.2 B).

Inferred pairwise interactions (α_{ij}) ranged from -9 to15 (Fig C.1) with the median varying from -1.1 to 2.3, encompassing both facilitative (negative sign) and competitive (positive sign) interactions (Fig 4.3). Based on the posterior we inferred both competitive and facilitative interactions among the same focal:neighbor pairs (Fig 4.3 and Fig C.1). We originally predicted that the colonial soft encrusting group, made up of colonial ascidians would be strong competitors. We found that this group showed a strong community effects, exerting strong competition as the focal individual having only competitive interactions with neighbors especially with solitary soft upright and solitary soft runner groups, two groups that would directly compete for primary space (Fig 4.3). Colonial soft encrusting group experienced weaker community response, with most focal functional groups exerting weakly competitive interactions on colonial soft encrusiting group, except facilitative interactions from solitary calcified upright group (Fig 4.3 A) which may provide space colonial soft encrusting to recruit onto. On the other hand, solitary soft runner group showed stronger community effects than its community response (Fig 4.3 A).

Three intra-group interactions were facilitative: solitary calcified upright, solitary soft upright, and colonial calcified encrusting groups. For example, solitary calcified upright organisms had a mean intra-group interaction of -1.31 ± 0.3. However, solitary soft runner group had strongly competitive interactions with itself (mean 1.91 ± 0.8) compared to other intra-functional group interactions. Our inferred pairwise interactions did not show a pattern of more competitive intra-specific interactions compared to inter-specific interactions as we would expect for equilibrium community with niche partitioning.

Simulations

In monoculture, functional groups reached a stable abundance regardless of initial density, except in the case of solitary soft runner group which showed explosive population dynamics, reaching an infinite population size when it started at an initial percent cover of one (Fig C.3). This initial percent cover of one may be unrealistic, as the maximum observed abundance of this group was 0.85. In all pairwise simulations groups reached a stable abundance within the time frame of the simulation. Colonial soft encrusting group reached the higher abundance than its competitor in all six if the possible pairings. While solitary calcified runner and solitary calcified upright groups showed lower (or the same) abundance than their competitor in all of their pairings (Fig C.4). The remaining groups showed varying results of simulated pairwise competitive dynamics (Fig C.4). Simulations of population dynamics revealed that in a diverse community containing all seven functional groups all groups were able to persist at median parameter values (Fig C.5). Similar to pairwise simulations, colonial soft encrusting group had the highest abundance of 0.25 which is lower than its pairwise abundances at a maximum of 0.6. While solitary calcified runner group had the lowest abundance, again lower than its maximum pairwise abundance (Fig C.5). In general, simulated populations reached a stable abundance under most scenarios with simulated abundances close to observed abundances suggesting that our population dynamics model is appropriate for these assemblages. This result of approaching an equilibrium agrees with observations in the field as recruitment to these assemblages waned towards the end of the study period.

Rankings and Trade-offs

We ranked functional groups according to median pairwise competitive abilities finding the colonial soft encrusting group to have the highest competitive rank and colonial soft upright group having the lowest (Table 4.2). These rankings did not predict the relative abundances seen in seven-species polyculture simulations.

We examined competition-colonization trade-offs among the functional groups studied here. Groups with larger inferred recruitment tended to exert less competitive effects resulting in lower community response (effect of, Fig 4.4A) but experience more competition resulting in larger community effect (effect on, Fig 4.4B). In general, as inferred recruitment increases,

TABLE 4.2: Ranking of functional group median competitive ability. A ranking of each functional group (R_i) is generated by summing the columns of the functional group interaction matrix (community response) and subtracting the sum of the rows (community effects), then taking the absolute value (Roxburgh and Wilson, 2000; Mouquet et al., 2004; Haddad et al., 2008; Carrara et al., 2015).

Functional Group	R_i
Colonial soft encrusting	7.56
Solitary soft runner	6.81
Solitary soft upright	3.93
Solitary calcified runner	3.01
Colonial calcified encrusting	2.76
Solitary calcified upright	2.49
Colonial soft upright	0.94

competition exerted by the group decreases and competition received by the group increases (Fig 4.4).

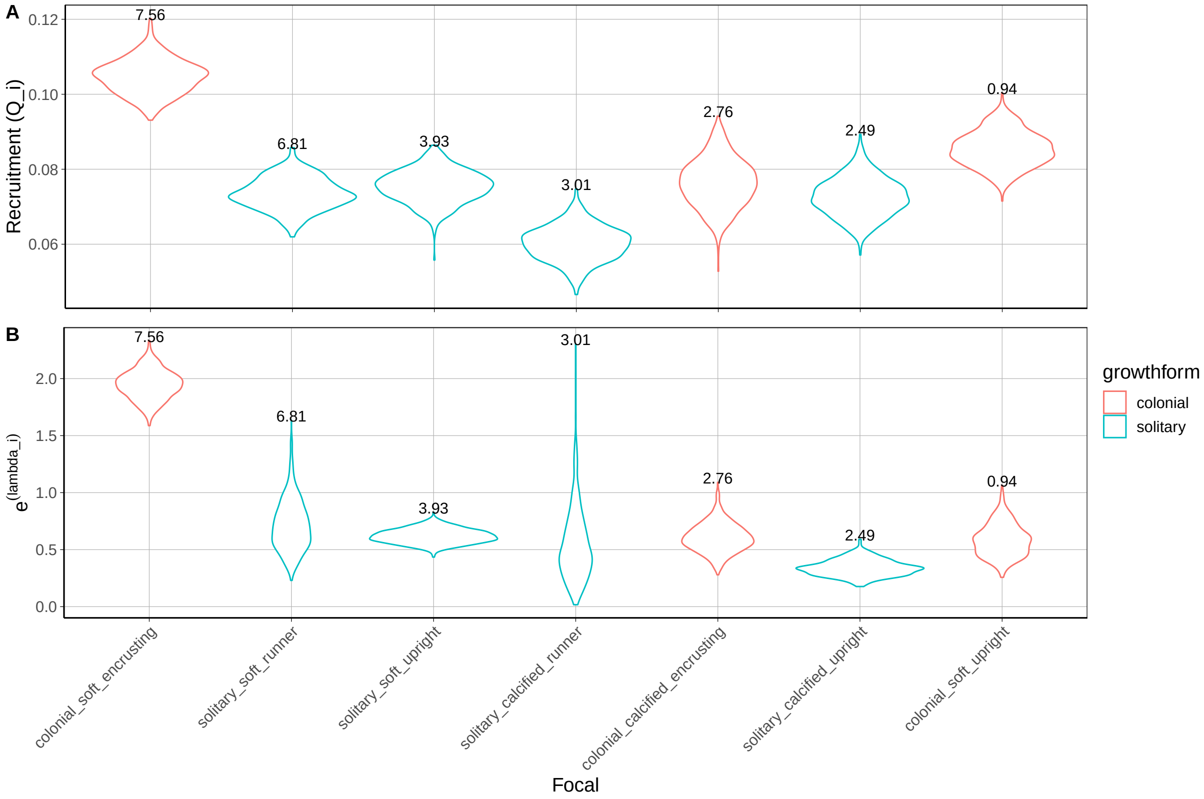

FIGURE 4.2: Inferred parameters. A) Posterior distribution of realized density-independent recruitment (Q_i) for each focal functional group. B) Posterior distribution of density-independent growth rate (e^{λ_i}) for each focal functional group. Based on 1000 posterior draws of the parameter. Groups are ordered left to right by highest to lowest competitive ranking (labelled above each violin). Competitive ranking does not have a clear trend with recruitment but more closely aligns with intrinsic growth. Colonial growth form often has higher inferred recruitment than solitary groups, while soft groups represent the highest and lowest intrinsic growth.

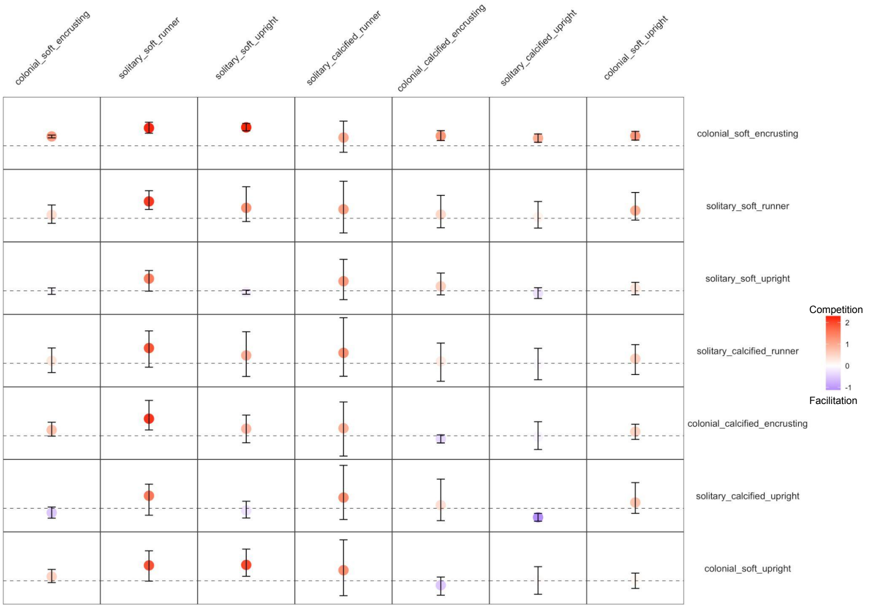

FIGURE 4.3: Inferred pairwise functional group interactions (α_{ij}). These interaction coefficients are responsible for density-dependent change in percent cover as part of Eqn 3 and later used to rank functional groups. Shows median model estimates of direct interactions among functional groups while error bars represent the 95% credible interval. Some interactions range from competitive to facilitative in their credible interval. Solitary calcified runner had the most variability in in its inferred interactions. Interactions along the diagonal represent intra-group interactions. Here competition is represented by positive coefficients and facilitation by negative coefficients. Groups are ordered left to right (or top to bottom) by highest to lowest competitive ranking.

Discussion

In this study, we used a combination of a field experiment, model parameterisation, and simulations to explore the mechanisms that promote coexistence in a space limited community. We found a hierarchy in competitive rank, with colonial soft encrusting group (colonial tunicates) as our top ranked functional group, in line with our original hypothesis. The three lowest ranked groups showed higher levels of inferred recruitment suggesting a trade-off between competition and inferred recruitment. This trade-off may have allowed susceptible functional groups to persist, suggesting that it plays a key role in structuring these assemblages. Marked differences in functional traits did not explain inferred population dynamics. In this context, similar responses observed among groups may be an important mechanism for their coexistence as moderate or relatively small inter-group interactions promote coexistence. By fitting the population dynamics model to empirical data, we also inferred a range of group-group interactions highlighting the prevalence of neutral and facilitative interactions. Taken together these results point to multiple, non-mutually exclusive mechanisms that promote coexistence among these benthic marine invertebrates.

Resource Partitioning is one of the simplest coexistence promoting mechanisms (Chesson, 2000b; Levine and HilleRisLambers, 2009). Benthic marine invertebrate communities are highly diverse with tens of phyla coexisting in densely packed communities (Buss, 1980; Palardy and

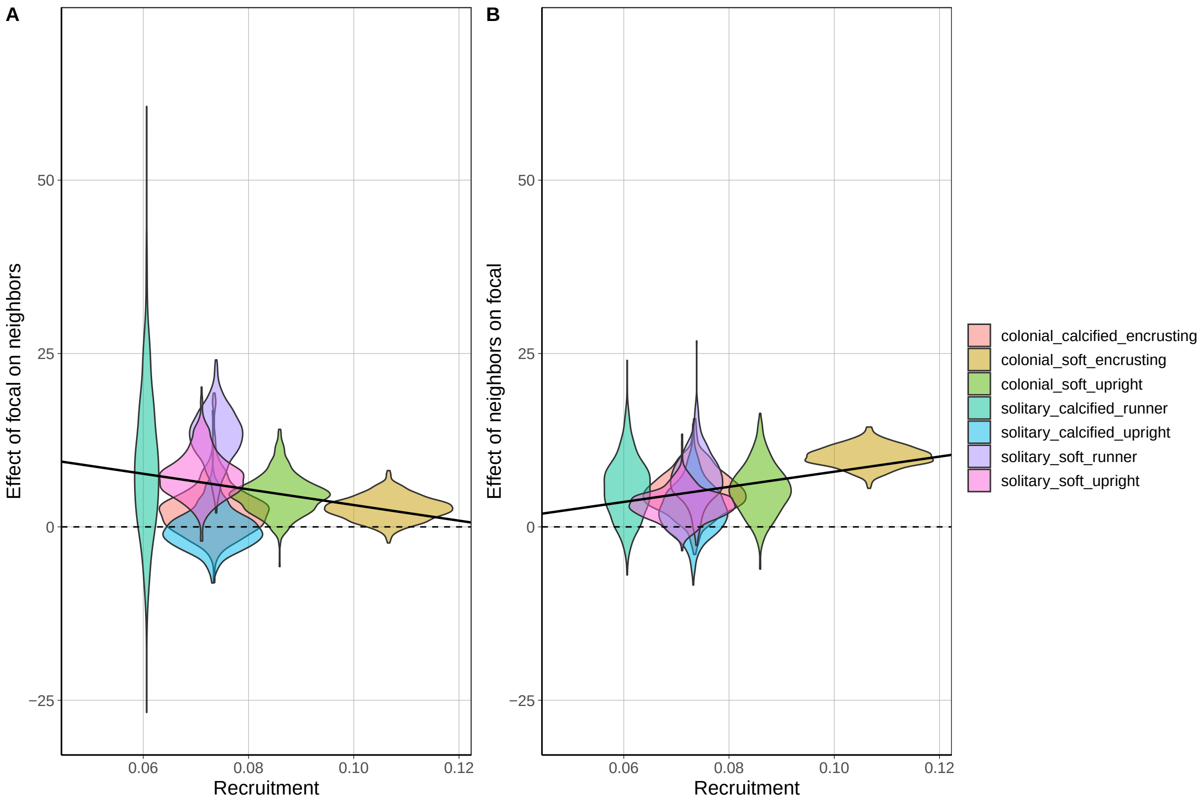

FIGURE 4.4: Competition-colonization trade-off of functional groups studied. A) Relationship between inferred recruitment (Q_i) and inferred effects of a focal functional group on neighbors as the column sums of our inferred pairwise interaction matrix (community response, $\sum \alpha_{ij}$). As recruitment increased competition exerted by the group decreased. B) How a group responds to the community, relationship between inferred recruitment (Q_i) and the effect of neighbors on a focal functional group as the row sums of our inferred pairwise interaction matrix (community effects, $\sum \alpha_{ji}$). As recruitment increases competitive interactions a group received increases. The difference between these two y-axes, effect of minus effect on, make up the ranking metric Eqn 4.4. Competition is represented by positive coefficients and facilitation by negative coefficients. Based on 1000 posterior draws of each parameter. A similar trade-off was explored for intrinsic growth rate C.2.

Witman, 2011). In addition to being space-limited, these communities may also compete for food and oxygen (Svensson and Marshall, 2015; Whalen and Stachowicz, 2017; Comerford et al., 2020) . Trait differences, such as growth form may allow groups to deferentially access resources and species strategies are determined by multiple interacting traits (Grime, 1973; Gross et al., 2007, 2015). For example, in this study solitary soft upright organisms can grow away from the benthic surface allowing them to access more food and oxygen than their encrusting neighbors. While the colonial soft encrusting group can better preempt space and resist overgrowth competition. The resulting interactions among these groups may be similar in outcome due to contracting trait combinations. For instance, soft-bodied organisms were ranked at both high and low competitively, similarly, colonial organisms held the top and lowest spot in the competitive ranking (Table 4.2). In this study, while the colonial soft encrusting group is deemed the dominant followed by solitary soft runner group, in seven species colonial soft encrusting group has the highest abundance followed by solitary soft upright group possibly reflecting its ability to compete in a different dimension (Fig C.5). The phenomenological nature of our model does not allow us to separate responses to different resources but our results highlight the usefulness of multiple trait axes and that these trait differences can act as equalizing mechanisms (Gross et al., 2015).

Trait-differences can also reflect strong average fitness differences. Life-history trade-offs, whereby the superior competitor has lower fecundity while the inferior competitors have higher fecundity, can provide a mechanism for coexistence allowing inferior competitors to persist in the system (Levins and Culver, 1971; Tilman, 1994; Bolker and Pacala, 1999). Here we found that as recruitment increased, competition exerted by a group decreased. For example, the colonial soft encrusting group had the highest inferred density-independent recruitment (Fig 4.2A) but some of the lowest community response interactions (effect of, (Fig 4.4A)). On the other hand, the solitary calcified runner group showed the lowest inferred recruitment and higher community response interactions (Fig 4.4A). Alternatively, this trade-off can be viewed in reverse or how a group responds to the community, here we found that as recruitment increased competitive interactions received by a group decreased or became weaker (Fig 4.4B). Colonial soft encrusting group had the highest community effects or received the most competition from neighbors. These trade-offs may help explain abundances seen in simulations (Fig C.5) and allow competitively inferior groups to persist.

Competition for space in closed contiguous patches of habitat—such as artificial substrates in marinas like those studied here—involve three primary mechanism: expansion- capturing empty space; lottery- short term responses to the sudden release of resources due to mortality; and overgrowth competition- a type of interference competition (Crowley et al., 2005). Studies suggest that displacement does not occur, i.e. if adults are invulnerable to displacement by propagules such as in our study or as trees are to seeds, competition-colonization trade-off alone is not enough to produce coexistence in a lottery system (Yu and Wilson, 2001). However, coexistence is possible with environmental heterogeneity or if the density of neighbors varies spatially and becomes a niche axis (Yu and Wilson, 2001). In our present study, assemblages initially varied in diversity and density of organisms (Marraffini and Geller, 2015) which could allow for competitively inferior organisms to find reprieve from strong competitive interactions or into assemblages with facilitative interactions. In our study of benthic marine invertebrate communities, we measured a range of interactions both competitive (positive) and facilitative (negative) even within the same focal:neighbor pair. The median of multiple interactions was inferred to be facilitative interactions (10 out of 49 pairwise interactions), while we observed majority facilitative interactions at the lower credible interval (Fig 4.3B). For example, the solitary calcified upright group had a median inferred intra-group interaction of -1.12 as well as facilitative interactions with two other groups: colonial soft encrusting and solitary soft upright. These facilitative interactions can be observed in the field were juvenile solitary calcified upright organisms such as mussels recruit to nearby adults and adults can even shift positions to be closer to other members of the same group (personal observation). If we think of variation in density and diversity of neighbors as environmental heterogeneity, it is not difficult to imagine that there are some patches of habitat where each group will find favorable biotic conditions.

Competition for space or spatially varying resources is nearly universal in ecological systems highlighting the importance of what drives coexistence in space-limited systems. Our approach of inferring population dynamics from empirical data highlights the varied nature of interactions among functional groups and the dynamics structuring coexistence in space-limited communities. Unfortunately, our study is limited—by nature—as it is unable to distinguish between individual responses to resources and represents a short time scale (2 months), perhaps too short to reveal competitive exclusion. Similarly by design, there are limitations with analytically evaluating equilibrium and stability of multispecies community in terms of a Ricker type model (Saavedra et al., 2017). Despite these limitations, simulated scenarios showed the relative abundance of functional groups reaching equilibrium and persisting in the community. These results taken together, led me to conclude that this space-limited community's coexistence is due to multiple, non-mutually exclusive mechanisms— multidimensional trait-differences, life-history trade-offs, and facilitation—allowing for the long-term persistence of this diverse system.

Acknowledgments

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Chapter 5

Discussion

Despite over a century of research, identifying factors that regulate populations and allow species coexistence remains a rich area of investigation. During the course of this thesis, my co-authors and I explored patterns that shape the distribution, abundance, and diversity of organisms across a range of natural systems. In my first chapter, I explored the role of direct and indirect impacts of global climate change on the population dynamics of perennial alpine plants across a global network of experiments. For my second, I investigated the role of indirect facilitation in the invasion success of annual flowering plants. Third, I explored population dynamics and persistence with the inclusion of facilitation in a diverse benthic marine invertebrate system. I used empirical data to understand theoretical concepts of community assembly and coexistence. Together the projects presented in this thesis, emphasize broadening coexistence investigations through the inclusion of both biotic and abiotic factors, facilitation, and indirect interactions. This work spans multiple ecological systems and processes highlighting the multifaceted nature of factors that drive distribution, abundance, and coexistence of populations.

Summary of Results

In my first thesis chapter, I explored the relative roles of an abiotic and a biotic driver on alpine-plant communities across multiple locations and elevations using a combination of empirical data and population-dynamics modeling. I found that, while some communities responded to our experimental manipulations of warming and removal of the dominant species, the cover of these communities remained relatively constant suggesting weak effects and the resilience of these communities. This pattern of no or weak treatment effects was seen in both our main population dynamics model and supplemental linear analysis. The relative importance of dominant species loss and warming temperatures varied among communities. None of the communities studied here showed exclusive support for a single treatment model, rather community dynamics were driven by multiple factors. Additionally, species within a community showed variable responses to experimental disturbances, as some responded similarly to the 'average' species at their site given by the grand mean, while others deviated strongly from this average. These species-specific responses, possibly due to varying life-history strategies of alpine plants (i.e. forb compared to C3 graminoid), may allow the overall community to persist in the face of environmental change even as some individuals decline. However, we did not detect any strong responses of individual growth forms. These results highlight the complicated nature of uncovering universal drivers of population dynamics and how these drivers will be altered by the scale of the observation (community- and population-level; single vs. multi-site) as well as by future and on-going disturbances such as climate change.

In the second chapter of my thesis, I examined the role of indirect interactions in diverse communities and how these interactions influenced introduced species fitness. Here I identify the presence of 'native turncoats': indirect facilitation of an introduced species by a native species (Northfield et al., 2015). To my knowledge, this is the first data-informed detection of these types of interactions in natural communities. While only one out of the five introduced focal species showed a benefit of 'native turncoats', these interactions had measurable effects on the fitness outcomes (fecundity) of the introduced species in question (*Petrorhagia dubia*). These results indicate that indirect interactions should not be simply ignored. Since there are always more indirect interactions than direct interactions in diverse systems, the relative importance of indirect interactions is greater even when they are small in magnitude. Results of this study emphasize the importance of both facilitation and indirect interactions on population dynamics to improve estimates and understand the persistence of species within a community. While 'native turncoats' likely only tell part of the story, the inclusion of indirect interactions in invasion ecology may help illuminate general patterns in spite of the 'invasion paradox'.

In the third chapter of my thesis, my results quantify the interactions among functional groups in a space-limited system inferring a range of facilitative and competitive interactions and evidence of competition-colonization trade-offs. Competition for space or spatially varying resources is nearly universal in ecological systems. Examination of space-limited communities is common with a long history of theoretical attempts to clarify the mechanisms underlying coexistence (Levins and Culver, 1971; Horn and MacArthur, 1972; Hastings, 1980; Tilman, 1994). By fitting the population dynamics model to empirical data, I also inferred a range of group-group interactions. Similar to previous studies, I found a hierarchy in competitive rank and a relationship between competition and inferred recruitment among functional groups. This trade-off allowed for susceptible functional groups to persist, suggesting that it plays a key role in structuring these assemblages. Marked differences in functional traits did not explain inferred population dynamics. In this context, similar responses observed among groups may be an important mechanism for their coexistence. Taken together these results point to multiple, non-mutually exclusive mechanisms—multidimensional trait-differences, life-history trade-offs, and facilitation—which promote coexistence among these benthic marine invertebrates.

General Implications

This thesis highlights the context-dependency and interplay among processes and mechanisms that control population structure and function. By incorporating multifaceted approaches like those implemented in this project, we can more accurately understand community assembly and coexistence. Cumulatively this work extends thinking about process influencing communities to include both abiotic and biotic factors, facilitation, and indirect interactions both independently and simultaneously. These results suggest that there is no one factor that controls population dynamics even within a single community and I suggest that we recognize the diversity of processes influencing community assembly and coexistence through more multifaceted approaches like those employed in this thesis.

This study merges theoretical models and empirical data to understand mechanisms of coexistence. The importance of parameterized models in the understanding of mechanisms of coexistence (Broekman et al., 2019) is becoming increasingly apparent as large scale environmental change generates novel communities and new species interactions (Alexander et al., 2016). However, it is important to note certain caveats with parameterized models: parameter fitting is data-intensive (Mayfield and Stouffer, 2017) and key ecological model parameters are often inseparable (Bolker, 2008; Song et al., 2019). Throughout this work, I made model and statistical choices to overcome data limitations. For example, in my first chapter, a model at one site failed to converge and another site had split model weight due to the limited number of observations. In the second chapter, I examined indirect interactions by categorizing these indirect neighbors as conspecific, native, or introduced rather than as individual species. This greatly reduced the number of parameters and since the general rule of thumb requires 10 observations per parameter to estimate, this technique drastically lessened the data required for this study. Data requirement is often a major obstacle in species interaction studies, using models with combined parameters allows us to lower this requirement without losing too much information. Additionally, the mixed-effect model frame-work employed in all of my chapters took advantage of random effects. Pooling of random effects can account for overdispersion and small or unequal sample size of some parameters (Janssen, 2012; McElreath, 2016; Nalborczyk et al., 2019). For instance in **Chapter** 2, I highlight the variability of species- and community-level responses by allowing treatment effects to vary with species using hierarchical models and a random effect. Similarly, I utilized this mixed effect framework in the following chapters to account for environmental variability (**Chapter** 3) and low and unequal sample size of interactions (**Chapter** 4).

In two of my chapters, to overcome the above-mentioned limitations, I used Bayesian framework to understand population dynamics of my study systems. This framework offers many advantages for using empirical data to parameterize coexistence models. A Bayesian framework is accommodating to unequal or small sample sizes (McElreath, 2016), can incorporate domain knowledge or hypotheses as priors (Clark, 2005; McElreath, 2016) and accounts for variability in population dynamics. As we begin to recognize the diverse and possibly interacting processes which shape ecological communities, posterior estimates in the Bayesian framework may provide better explanations for the patterns of abundance and diversity seen in nature. For example, in my third chapter, many of the pairwise interactions measured ranged from competitive to facilitative. While this could be interpreted as that pair having no or neutral interactions, it could also be a result of unmeasured variability (Clark, 2005). For example, one can imagine the presence of another organism in some communities changing the direction of this pair's interaction (Levine et al., 2017b) or microhabitats which slightly vary in environmental conditions (Bimler et al., 2018; Shoemaker et al., 2020b) as interspecific interactions are known to change from negative (competitive) under benign environmental conditions to positive (facilitative) under stressful conditions (Callaway, 1995; Bruno et al., 2003a). While Bayesian framework can not always point to mechanisms for this variability, it does allow us to carry it through to our predictions about community coexistence and diversity. Thereby shifting coexistence predictions from a question of 'if' to a question of 'under what conditions'.

Inclusion of facilitative and indirect interactions into invasion ecology helps highlight the diversity of mechanisms by which a community may coexist and prevent introductions. For two competing species to coexist their intraspecific competition must exceed their interspecific competition, based on Lotka-Volterra models of two-species competition (Case and Roughgarden, 2000; Chesson, 2000b; Gotelli et al., 2008). However, this simple intuition does not account for facilitative interaction nor dynamics that emerge in multispecies communities. Coexistence between pairs of species does not necessarily translate to multispecies community coexistence (Levine et al., 2017b; Saavedra et al., 2017; Song et al., 2019) and a range of mechanisms can allow for coexistence where pairwise coexistence is not possible (Levine et al., 2017b; Gallien et al., 2017; Kleinhesselink et al., 2019; McPeek, 2019). In Chapter 2, I examine one such mechanism, indirect facilitation. Similarly, my results from Chapter 3, highlight the importance of facilitative and multispecies interactions to community persistence even in the presence of a competitive hierarchy. In both chapters the effects of multispecies interactions are not consistent nor necessarily predictable, reiterating the value of analyzing parameterized models (Siepielski and McPeek, 2010; Terry et al., 2020) and highlighting how different mechanisms may be contributing to community assembly and coexistence within a single community.

Future Directions

If we want to provide a general understanding of community coexistence we need to develop new frameworks. These frameworks should be guided by theory, applicable across multiple mathematical formulations, and be coupled with observational and/or experimental communities to test and refine our predictions. I provide a case for the inclusion of multiple, non-mutually exclusive mechanisms that promote coexistence into these frameworks including: individual variability (**Chapter** 2), facilitation, as well as the types of interactions that emerge in multispecies communities (**Chapter** 3).

Parameterisation of population-dynamics models with empirical data to allow for not only accurate predictions but also to explore the parameter space which may offer opportunities for coexistence even when mean estimates do not. This lesson can be applied to future studies, to explore this parameter space in order to offer insights into which conditions allow for coexistence and diversity seen in nature. For example, if there is an empirical dataset of two plant species grown at different combinations of densities. You could fit a Beverton-Holt or similar model to the data and then use the inferred parameters to calculate invasion growth rates then evaluate evidence of and mechanisms for stable coexistence. If these species were grown with soil from either the same plant or the opposite plant species you could make inferences about the role of generalist and specialist microbes as a mechanism for stable coexistence. Recent perspectives and reviews have offered a useful framework for designing empirical experiments

(Broekman et al., 2019; Godwin et al., 2020) and simulation studies (Ellner et al., 2019; Shoemaker et al., 2020a) on measuring mechanisms of coexistence. However, these fall short when it comes to multispecies interactions and facilitation.

The vast majority of our definitions and modeling frameworks for understanding species coexistence focus on two-species communities with competitive interactions for shared resources (Spaak and De Laender, 2020). However, ecology is moving towards larger, multifactorial studies as we attempt to understand ecological communities and their functions while developing predictions about their changes under increased biotic and abiotic stressors such as invasions and global change. Recent studies have extended our two-species thinking to more diverse systems with the aid of new theoretical approaches (Saavedra et al., 2017; Song et al., 2019). I broaden this thinking by incorporating facilitative interactions among multispecies communities. Estimating interaction strengths allows us to better understand multispecies (3 or more species) community dynamics and provide more accurate estimates of community changes in response to climate change (Alexander et al., 2016), niche differences (Adler et al., 2007), and ecosystem stability (Tang et al., 2014). Going forward, an extension of this work incorporating multispecies dynamics would be to use a model parameterization framework to better link observed processes to underlying mechanisms, evaluate their relative importance, and advance our understanding of coexistence and diversity. For instance, imagine there are experimental data on the per capita population growth rates of multiple species growing in combinations of varying density and richness. This data would allow us to infer species interactions among the species. If this data also spanned environmental gradients we could examine the changes in interactions with abiotic factors and link observed relative abundances to mechanisms of coexistence. Recent work has shown that community-level stabilization and adjusted fitness differences can be used to make predictions about coexistence that are not susceptible to higher-order interactions and intransitivity (Barabás et al., 2018; Chesson, 2018). Additionally, structural approaches to coexistence can be extended to include facilitative interactions (Saavedra et al., 2017). Through simulation experiments, we can test predictions of coexistence across different environmental gradients to examine questions about how future climate change may impact our predictions of coexistence and the relative importance of fluctuation-dependent and fluctuation-independent mechanisms for coexistence.

Conclusions

In this doctoral thesis, I leverage empirical datasets and population dynamics models to better understand factors that influence ecological communities. This project provides insight into the roles of abiotic and biotic factors, facilitation, and multispecies interactions in community dynamics. With predicted increases in global climate change and introduced species, there will be changes in community assemblages and structure as well as the creation of novel assemblages with no evolutionary history. Understanding factors that drive communities is essential. This study demonstrates novel insights into community dynamics by including the roles of individual variability, facilitation, and indirect interactions in model estimates. Particularly incorporating environmental variability, variability in interaction strength and direction, and the types of interactions that emerge in a diverse community into our frameworks. More data about species interactions and experiments explicitly designed to measure interactions and co-existence will hopefully contribute to solving still one of the major questions in ecology: ‘how are there so many organisms’?

Part II

Appendices

Appendix A

Supplemental Material: Variable responses of alpine-plant communities to warming and loss of dominant species

Methods

The data used in this study form part of a larger study of alpine plant communities that combines experimental warming and dominant plant species removal among multiple globally-distributed elevation gradients (WaRM: Warming and (species) Removal in Mountains) (Classen, 2019).

FIGURE A.1: View of the Colorado, US field site. Shows open-top chambers in place over experimental plots.

TABLE A.1: MetaData for sites. Number of species records the number of species investigated in the model. Approximate length of the growing season. Average percent cover of a plot at the site including all species originally present. Amount modelled shows the average community percent cover in a plot actually included in the model after exclusions (i.e. those that were considered widespread species by our criteria) described in the methods.

Location	Elevation (meters)	Latitude	Longitude	Growing season (months)	Number of species	Average Percent Cover	Percent Cover Modelled
CA	Low (1431)	60.979	-138.408	3	16	82.9	64.1
	High (1900)	60.954	-138.423	3	7	59.7	38.4
CH	Low (2101)	46.77497	9.862969	4	12	126.0	83.0
	High (2353)	37.707	101.372	4	12	108.0	78.5
CN	Low (3200)	37.617	101.200	4	19	127.0	89.5
	High (4004)	46.774113	9.856959	4	11	146.0	81.8
NZ	Low (1071)	-39.296	175.727	6	26	106.0	85.9
	High (1611)	-39.285	175.623	6	9	29. 3	12.8
US	Low (2740)	38.715	-106.823	3	18	88.7	53.8
	High (3460)	38.992	-107.067	3	18	96.6	73.9

Dominant Species

The dominant species at each site was not included in analyses for three main reasons. First, it is statistically complicated to include this as the model estimates the individual parameters for each species under each treatment but the dominant is inherently absent from two of the treatments. Second, by removing the dominant we lose little information about the remaining plots since they account for between 10.2 and 52.3, with a median of 20 percent cover in non-removal plots at each sites (Table A.2). While these may seem like large numbers, total cover in plots ranged from 33.5 to 121.7 percent cover.

TABLE A.2: Average percent cover of the dominant species per plot at each site compared to cover of the total community. Shows average percent cover in each treatment (across all plots and years studied), as well as its average percent cover before exclusion in the removal and removal:warming treatment. These values are an average of all years and are expected to be low in removal treatments due to years of removal of adults. Total Community shows the average percent cover of a plot summed across of all species (including the dominant species).

Location	Elevation	Species	Ambient	Warming	Removal	Removal:Warming	Total Community
CA	Low	Salix reticulata	19.87	14.4	7.06	6.69	88.48
	High	Carex consimilis	28.0	30.5	10.5	9.47	58.91
CH	Low	Vaccinium uliginosum	33.2	52.3	16	18.6	121.7
	High	Vaccinium uliginosum	34.1	35.6	15.3	12.5	111.87
CN	Low	Stipa aliena	11.6	14.6	12.6	12.3	109.10
	High	Kobresia pygmaea	10.2	12.1	12.1	6.95	113.49
NZ	Low	Calluna vulgaris	18.1	23.5	7.83	7.88	108.77
	High	Gaultheria collensoi	29.1	21.8	6.43	4.78	33.5
US	Low	Wyethia amplexicaulis	20.2	37.87	5.03	4.08	80.94
	High	Juncus drummondii	21.6	16.07	3.22	2.33	87.97

Third, analysis of these species in non-removal treatments at their respective sites revealed that their dynamics do not vary as a function of the warming treatment; therefore, their inclusion in the analysis would not alter the overall conclusions about community dynamics. In two of the ten sites, the warming treatment influenced the dominant: in the US (high elevation) and CH (low elevation), based on the same model weighting procedure as in the main text (see Methods: Model Comparison). Despite this support for warming treatment in the best-fit model, warming the dominant species showed small changes in growth as a response. For example, at low elevation CH density-dependent change in cover increased from $\exp(g|A) = 0.42$ under Ambient conditions to $\exp(g|W) = 0.52$ under warming conditions.

Wide-spread species

As noted in the Methods, we also concentrated our analysis on the most widespread species within each site. We defined widespread as the species observed in at least 25 percent of total plots (for example: 0.25×32 plots $\times$ 4 years = 32 plots, which becomes the minimum number of plots a species must be present in to be analyzed). The resulting number of plots varied by location depending on the number of years studied (Supplemental Table A.1). We tested the robustness of this threshold, and found that fitting the model to species in 20 and 30% of plots showed qualitatively consistent results at the site level (results not shown). While these widespread species represent a subset of the total species observed, they account for the majority of the percent cover observed in the plots (Table A.1; Figs A.2 and A.3).

Results

Community level results

Models utilized here performed well across a range of observations, species richness (7–26), and plant species across sites (Low Main Text Fig 2.1 and High Fig A.5).

Species-specific results

Species responded idiosyncratically to treatments and showed differing rates of influx of species. While in some sites responses of individual species to treatments mimicked the grand means (e.g. Fig A.8), theses species still showed a range of changes in percent cover. In some sites an individual species showed a relatively large change in its percent cover in response to the removal of the dominant species (for example) even though the grand means at that site showed minimal responses to treatments (e.g. Fig A.6). These results illustrate that response of the whole community does not dictate the response of individual species. Figures presented for each site below. Sites with support for multiple models have are depicted with averaged posteriors predictions. If a treatment was not supported in the best-fit model(s) that treatment represents the ambient effect if a single treatment or the single treatment if the combination effect.

Density-independent influx also varied by site with NZ having the lowest average contribution to species cover and CN having the highest. Other sites received around 1% influx. Density-independent influx of species in these communities which may have resulted from an influx of seeds, germination of seeds from the seed bank, or lateral encroachment of neighboring plants. While a small amount, given density-dependent change in cover of less than 1 in some areas, influx may be allowing plots to maintain cover.

TABLE A.3: Fixed effects of linear mixed effects models showing the relationship between change in percent cover and treatments. ANOVA showed no effect of treatment (F(3,251)=1.202, p=0.31)

Factor	Value	Std. Error	DF	t-value	p-value
Control	12.66	12.78	244	0.99	0.32
Removal	4.09	4.41	244	0.929	0.35
Warming	-5.78	4.39	244	-1.31	0.18
Removal:Warming	4.84	4.39	244	1.10	0.27

Linear Regression Analysis

We examined the change in cover as the total cover of a plot (the sum of all species' percent cover) as final (last year measured) minus initial (first year measured). China is not represented as many plots in this location were not recorded in the first and last year leading to a low and unbalanced sample. We used an ANOVA to determine if there were any differences among treatment across all locations and found no effects of treatment (ANOVA, F(3,251)=1.202, p=0.31, Fig. A.4). To examine the effects treatments within sites, we used a linear mixed effects model with elevation nested within location as a random effect. This test did not reveal any significant effect of treatment (Table A.3).

Functional Group Analysis

To examine how treatments affected groups of plants rather than individual species, we lumped plants into their functional form: C3 graminoid, forb, legume, and woody shrub based on taxonomic identifications. Similarly to focal-species analysis preformed in the main text, we used a population-dynamics model for percent cover of a functional group as a function of previous percent cover. Here our model format allows for varying effects of each functional group that correspond to deviations from the grand mean (Δ parameters). Unlike species specific analysis, since there are inherently fewer functional groups we were able to combine data across sites and analyze the effect of site (elevation within location) as a random factor with ten levels. Again, we used a Beta distribution to generate predicted cover since our observations are always a series of non-negative integers and weakly informative priors for all of the parameters. We modeled cover with our linear mathematical model of population dynamics (Eqn 2.1 and 2.2 in the main text), we used weakly informative priors to parametrize the treatment (control, R, W, and RW) terms within growth (Eqn 2.2 in the main text) since we had no previous knowledge with which to constrain these parameters. We performed sampling to determine the posterior distributions of model parameters through the function "brm" from the package "brms" (Bürkner, 2017) in the statistical program R (version 3.4.2) (R Core Team, 2013). We ran two chains with a warm-up of 1000 iterations and 3000 sampling iterations each, and this produced a final combined posterior of 6000 MCMC samples for each model. We determined that parameters converged when trace plots were well mixed and stationary, and the Gelman-Rubin convergence diagnostic equaled one (Gelman and Rubin, 1992; Brooks and Gelman, 1998). As with the species specific analysis, we compared a series of models (developed in a step-wise fashion from least parameterized to most) to examine the relative importance of each treatment

TABLE A.4: WAIC comparison of candidate models on functional group data. The Null model received the most support and warming was the only treatment to receive any support with 5% of the weight. These models are the same formulation as the main text Table 1 but here i in Δ_i refers to a functional group. Model comparisons is also the same procedure as the main text (see Methods: Model Comparison section)

Model Name	WAIC	pWAIC	Weight
Null	-1561.12	64.58	0.83
Ambient	-1557.25	69.12	0.12
Warming	-1555.47	72.87	0.05
Removal	-1548.63	55.98	0
Removal + Warming	-1547.86	61.19	0
Removal × Warming	-700.43	4.99	0

and treatment combination to variation in population dynamics (see main text Table 1). Best-fit models were those with the lowest WAIC and an Akaike weight greater than 0.8.

This analysis focused on five functional groups (forb, C3 Graminoid, woody shrub, legume, and moss) as a random effect similar to the analysis in the main text where focal species was a random effect. Additionally this analysis included a random effect for site. Here the winning models was the null model (0.83 WAIC weight). Showing no support for any treatment at the functional group level. The recruitment models did not converge in this analysis.

TABLE A.5: Species list by elevation shows species and functional group assignments for the species investigated at each site.

Location	Elevation	Taxa	Functional Group
CA	Low	*Achillea millefolium*	Forb
		Aconitum delphinifolium	Forb
		Anemone spp.	Forb
		Artemesia norvegica	Forb
		Carex spp.	C3 Graminoid
		Castilleja spp.	Forb
		Festuca altaica	C3 Graminoid
		Lupinus arcticus	Legume
		Mertensia paniculata	Forb
		Myosotis alpestris	Forb
		Polemonium pulcherrimum	Forb
		Senecio lugens	Forb
		Valeriana capitata	Forb
		Veronica wormskjoldii	Forb
	High	*Equisetum variegatum*	Forb
		Pedicularis spp.	Forb
		Petasites frigidus	Forb
		Salix reticulata	Woody
		Salix rotundifolia	Woody
		Saxifraga oppositifolia	Forb
		Senecio atropurpureus	Forb
CH	Low	*Avenella flexuosa*	C3 Graminoid
		Calamagrostis villosa	C3 Graminoid
		Homogyne alpina	Forb
		Luzula sieberi	C3 Graminoid
		Oxalis acetosella	Forb
		Empetrum nigrum subsp. *hermaphroditum*	Woody
		Rhododendron ferrugineum	Woody
		Rumex alpestris	Forb
		Vaccinium myrtillus	Woody
		Vaccinium vitis-idaea	Woody
	High	*Anthoxanthum alpinum*	C3 Graminoid
		Arnica montana	Forb
		Carex curvula	C3 Graminoid
		Diphasiastrum alpinum	Moss
		Empetrum nigrum subsp. *hermaphroditum*	Woody
		Gentiana punctata	Forb
		Helictotrichon versicolor	C3 Graminoid

		Hieracium alpinum	Forb
		Homogyne alpina	Forb
		Leontodon helveticus	Forb
		Ligusticum mutellina	Forb
		Loiseleuria procumbens	Woody
		Luzula lutea	C3 Graminoid
		Nardus stricta	C3 Graminoid
		Phyteuma hemisphaericum	Forb
		Senecio incanus	Forb
		Vaccinium myrtillus	Woody
CN	Low	*Ajania tenuifolia*	Forb
		Aster flaccidus	Forb
		Elymus nutans	C3 Graminoid
		Euphrasia regelii	Forb
		Gentiana aristata	Forb
		Gentiana straminea	Forb
		Gueldenstaedtia diversifolia	Legume
		Kobresia humilis	C3 Graminoid
		Lancea tibetica	Forb
		Leontopodium nanum	Forb
		Morina chinensis	Forb
		Oxytropis qinghaiensis	Forb
		Poa crymophila	Forb
		Potentilla bifurca	Forb
		Potentilla saundersiana	Forb
		Saussurea nigrescens	Forb
		Saussurea superba	Forb
		Stellaria umbellata	Forb
		Taraxacum mongolicum	Forb
		Thalictrum alpinum	Forb
		Thalictrum rutifolium	Forb
	High	*Allium sikkimense*	Forb
		Anaphalis lactea	Forb
		Aster flaccidus	Forb
		Carex przewalskii	C3 Graminoid
		Kobresia humilis	C3 Graminoid
		Lancea tibetica	Forb
		Leontopodium nanum	Forb
		Oxytropis qinghaiensis	Legume
		Pedicularis kansuensis	Forb
		Poa crymophila	C3 Graminoid
		Poa orinosa	C3 Graminoid

		Potentilla saundersiana	Forb
		Rheum pumilum	Forb
US	Low	*Achillea millefolium*	Forb
		Alopecurus pratensis	C3 Graminoid
		Elymus elymoides	C3 Graminoid
		Eremogone congesta	Forb
		Erigeron sp.	Forb
		Erigeron speciosus	Forb
		Festuca thurberi	C3 Graminoid
		Galium septentrionale	Forb
		Poa fendleriana	C3 Graminoid
		Potentilla gracilis	Forb
		Rosa woodsii	Woody
		Taraxicum officinale	Forb
		Tragopogon dubius	Forb
		Vicia americana	Legume
	High	*Agoseris glauca*	Forb
		Arctostaphylos uva-ursi	Woody
		Arnica mollis	Forb
		Carex ebenea	C3 Graminoid
		Castilleja sulphurea	Forb
		Draba spectabilis	Forb
		Erigeron glacialis	Forb
		Erythronium grandiflorum	Forb
		Poa alpina	C3 Graminoid
		Poa arctica	C3 Graminoid
		Senecio crassulus	Forb
		Sibbaldia procumbens	Forb
		Viola labradorica	Forb
NZ	Low	*Asteraceae*	
		Celmisia glandulosa	Forb
		Celmisia gracilenta	Forb
		Celmisia spectabilis	Forb
		Chionochloa pallens	C3 Graminoid
		Chionochloa rubra	C3 Graminoid
		Coprosma cheesemanii	Woody
		Coprosma perpusilla	Woody
		Dracophyllum recurvum	Woody
		Dracophyllum subulatum	Woody
		Epacris alpina	Woody
		Euphrasia cuneata	Forb
		Gaultheria colensoi	Woody

	Gonocarpus micranthus	Forb
	Veronica tetragona subsp. *subsimilis*	Woody
	Veronica venustula	Woody
	Leucopogon fraseri	Woody
	Orchids	Forb
	Oreobolus strictus	Forb
	Pentachondra pumila	Woody
	Poa colensoi	C3 Graminoid
	Wahlebergia pygmaea	Forb
High	*Anistome aromatica*	Forb
	Celmisia gracilenta	Forb
	Chionochloa pallens	C3 Graminoid
	Gentianella bellidifolia	Forb
	Luzula colensoi	Forb
	Muehlenbeckia axillaris	Woody
	Poa colensoi	C3 Graminoid
	Raoulia albosericea	Forb
	Wahlebergia pygmaea	Forb

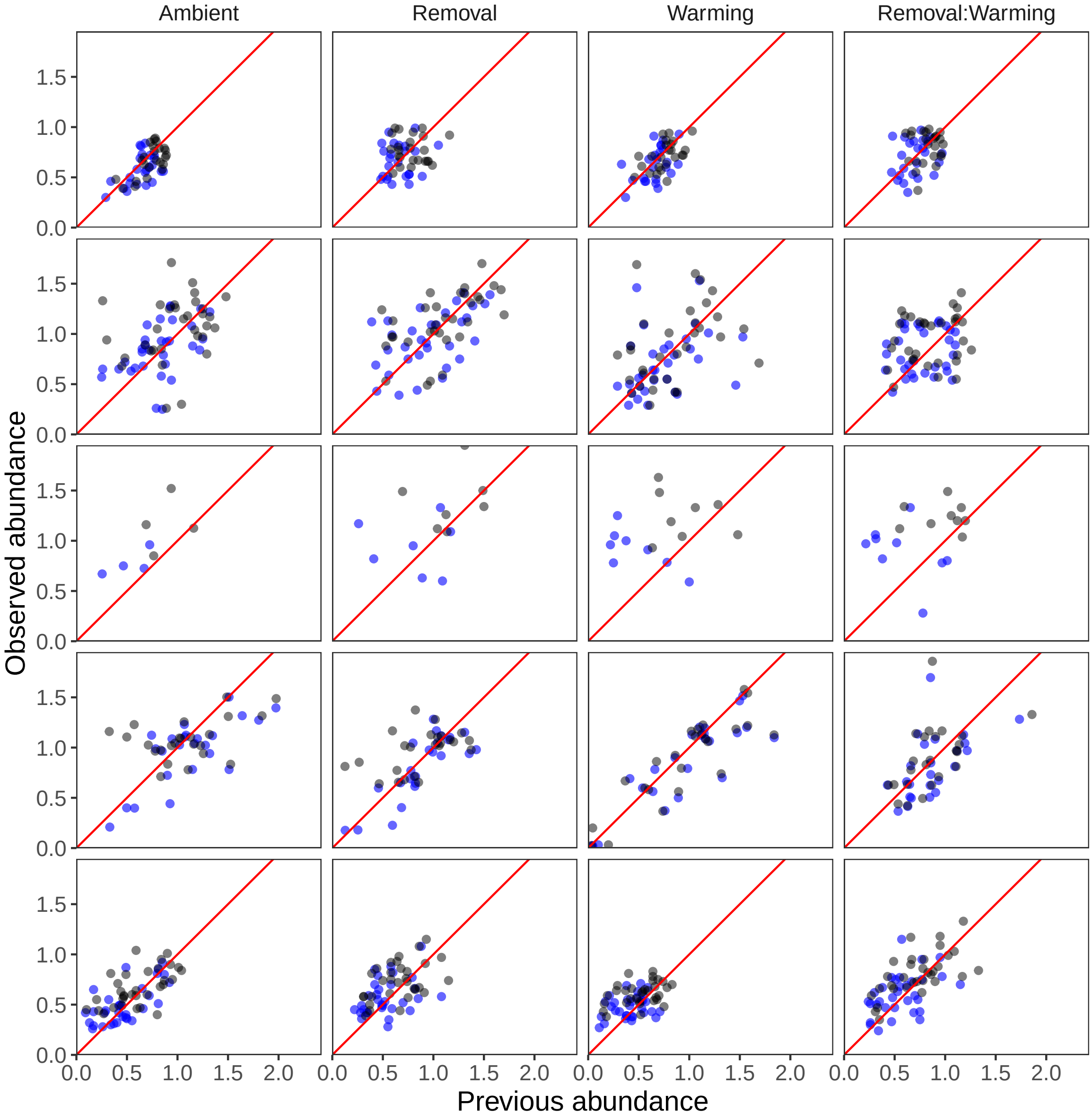

FIGURE A.2: Raw and modeled data on a plot level at each site at the low elevation. Shows total percent cover in a plot as gray dots and the percent cover used in the analysis (after removal of the dominant species and less widespread species) as blue dots. The red line represents 1:1 or where previous cover would equal current cover ie when plots neither grow nor decline in percent cover.

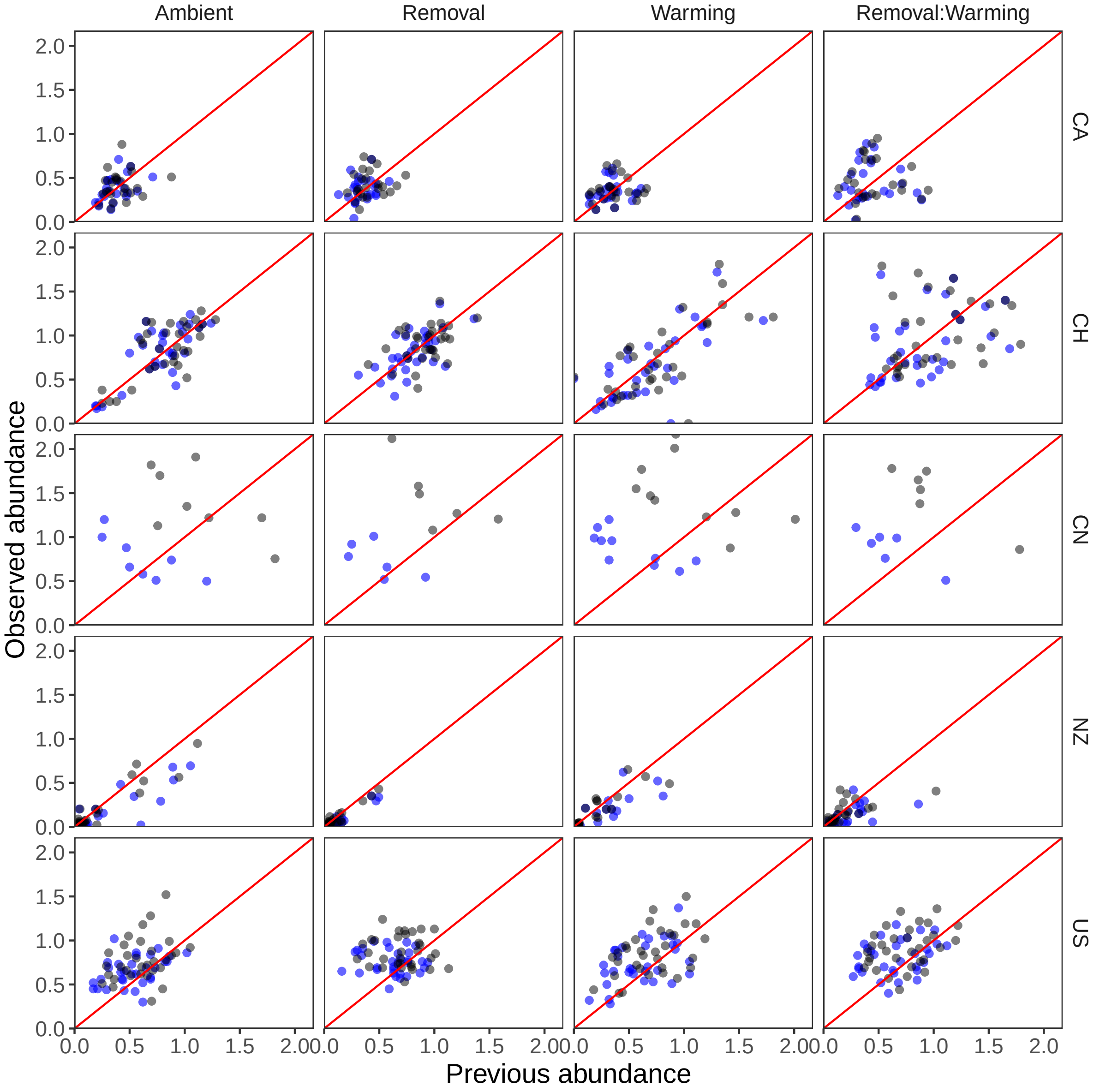

FIGURE A.3: Raw and modeled data on a plot level at each site at the high elevation. Shows total percent cover in a plot as gray dots and the percent cover used in the analysis (after removal of the dominant species and less widespread species) as blue dots. The red line represents 1:1 or where previous cover would equal current cover ie when plots neither grow nor decline in percent cover.

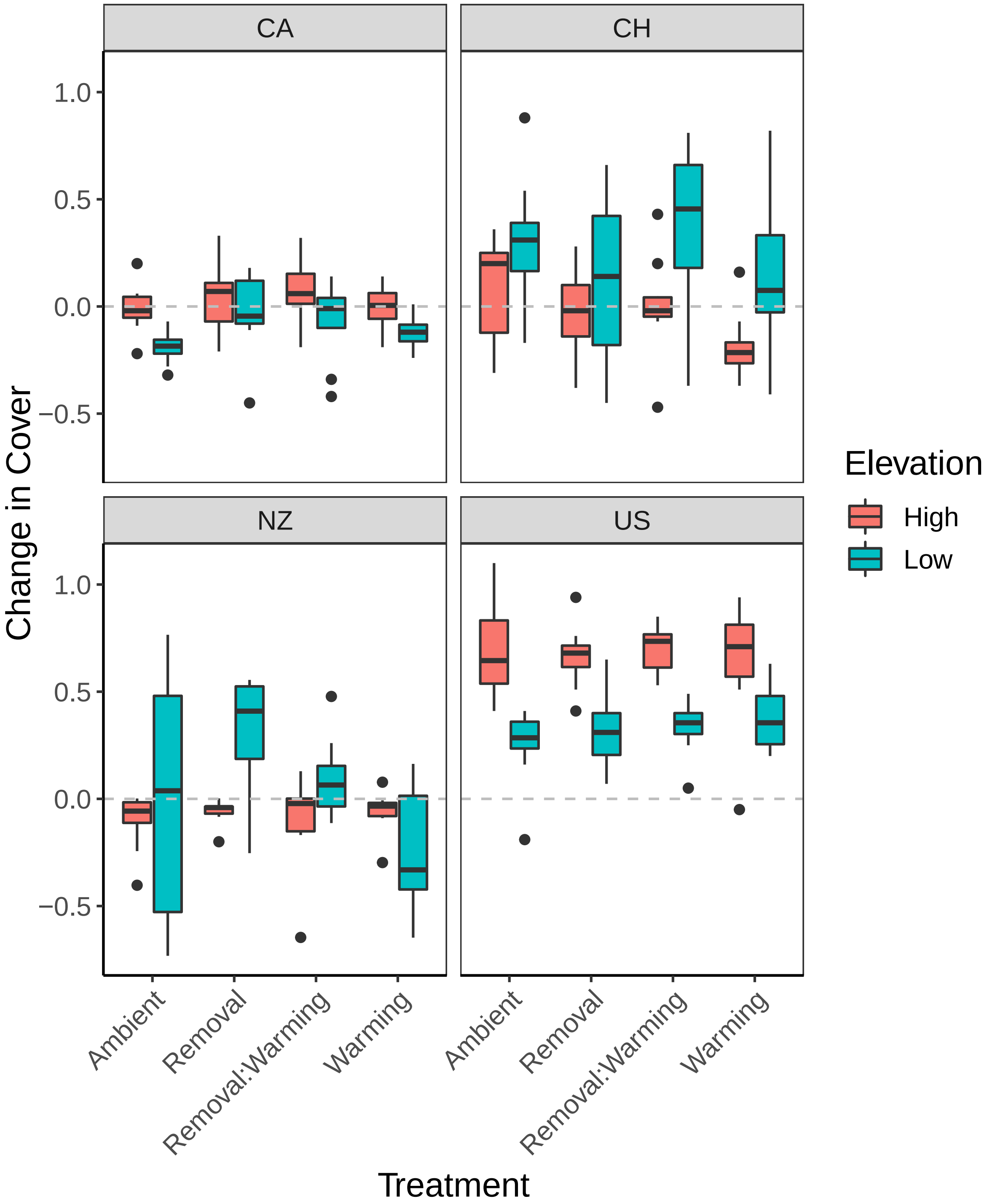

FIGURE A.4: Change in percent cover within plots across treatments and sites. Change is calculated as final (last year measured) minus initial (first year measured). Percent cover of all species is summed to reveal one value for each plot. China is not represented as many plots in this location were not recorded in the first and last year.

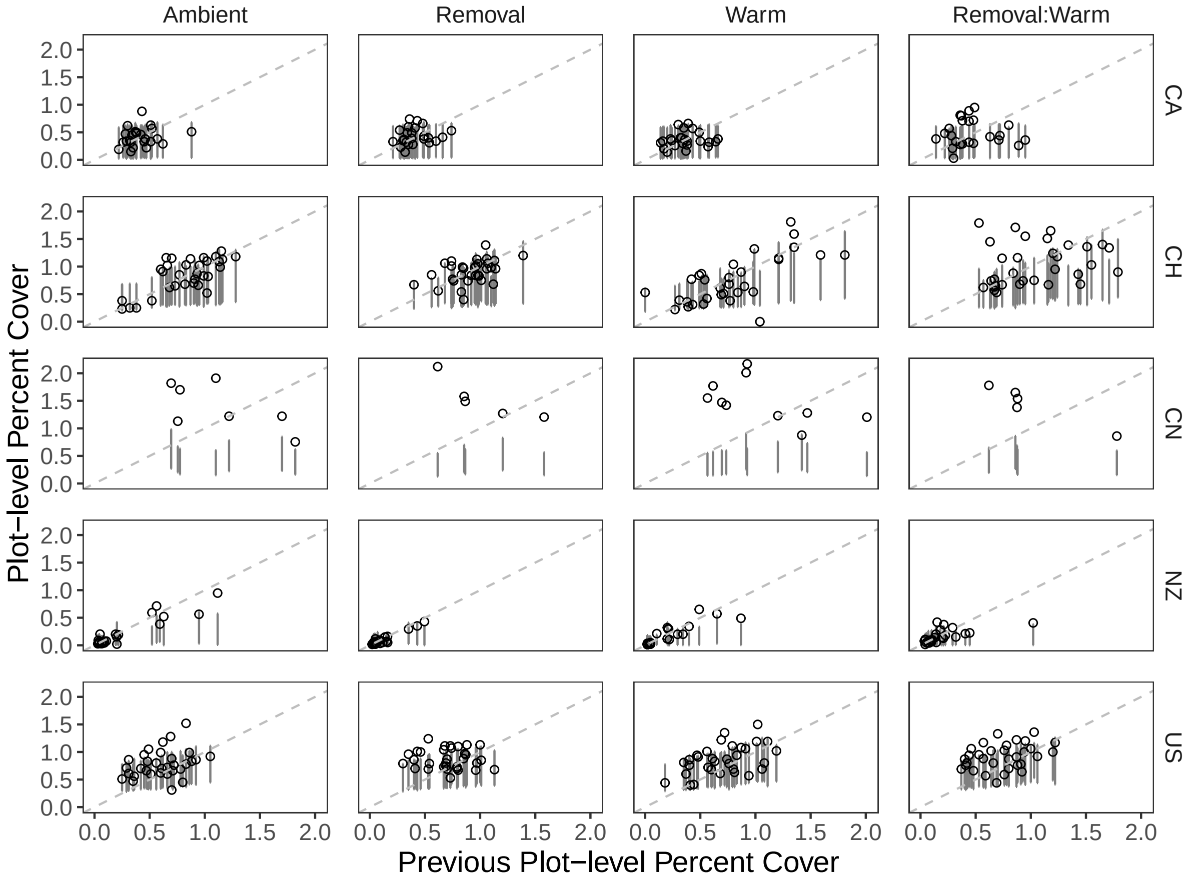

FIGURE A.5: Predicted and observed cover for all plots in high elevation across sites. Shows the model fit by overlaying predictions on top of observations. Points show the total observed cover in a plot, while shaded bars shows confidence interval (89%) of the predicted total cover for that plot. Predicted cover is calculated according to Eqn 2.1 then summed for each species within a plot to yield a plot level predicted cover. The dashed line represents 1:1 or where previous cover would equal current cover i.e. when plots neither grow nor decline in percent cover.

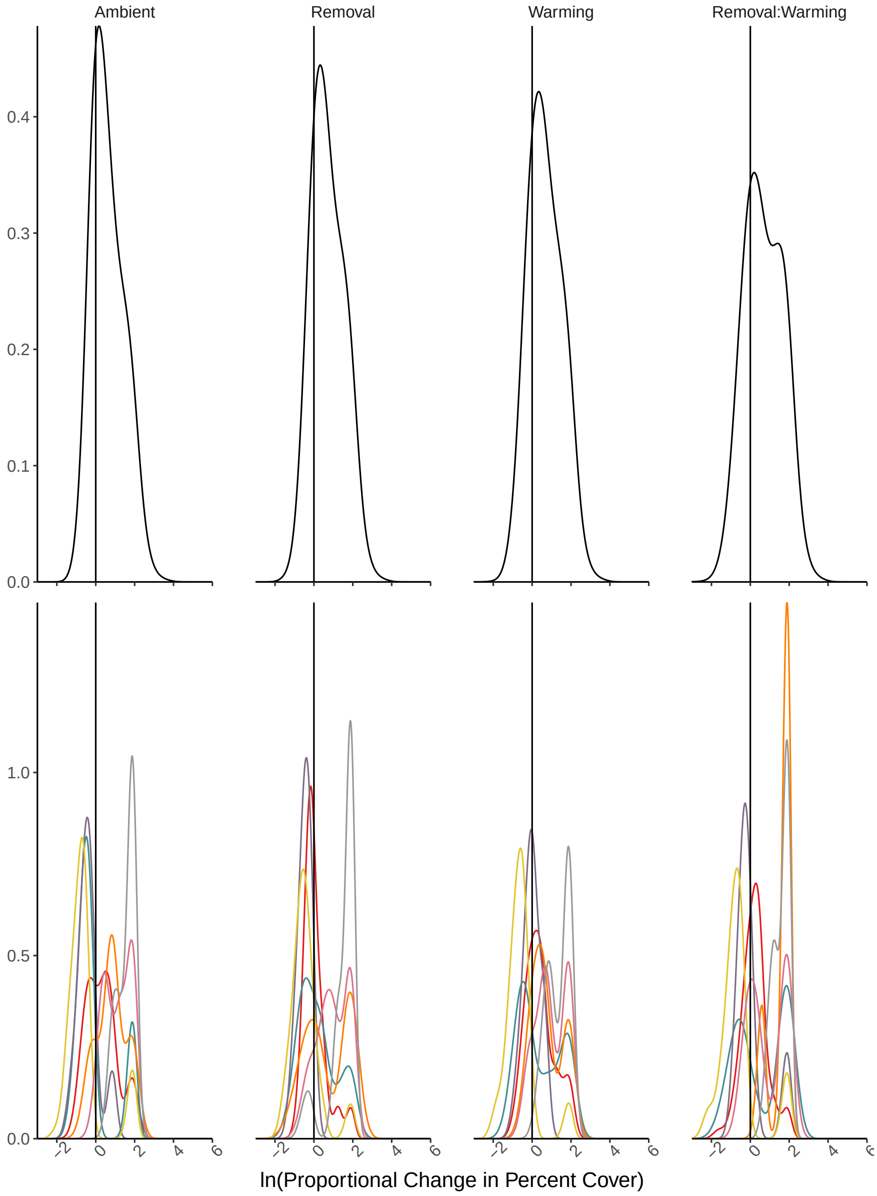

FIGURE A.6: Probability density of proportional change in percent cover within the high elevation Canada site. Logarithmic proportional change in cover is calculated as $(\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}}))$ as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species, which in this case only shows minor effects of the removal treatment. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site has support for multiple models and the posterior predictions were averaged across winning models: Ambient, Warming, and Removal. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

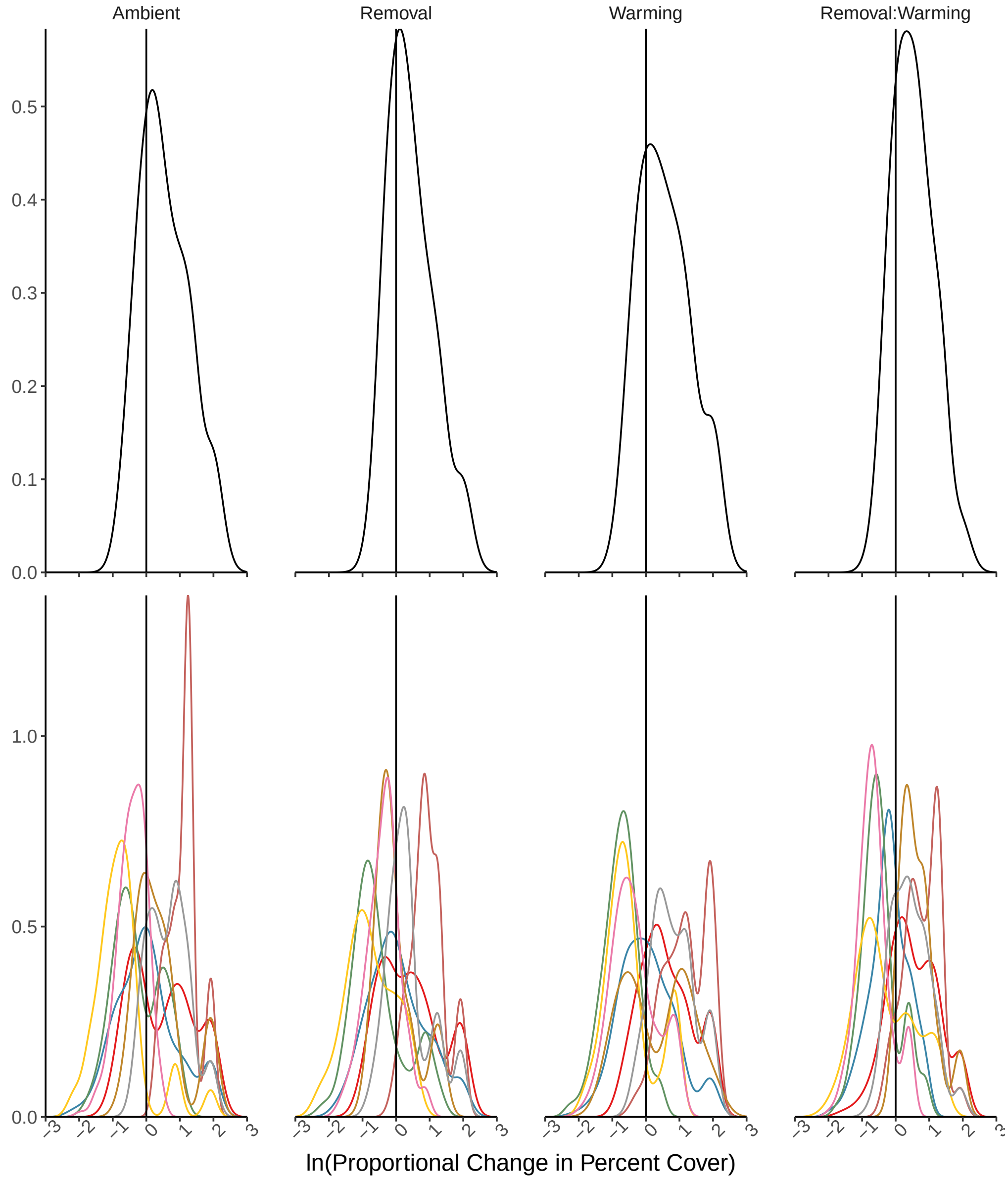

FIGURE A.7: Distribution of predicted change in percent cover within the low elevation Swiss site. Logarithmic proportional change in cover is calculated as $(\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}}))$ as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero $(\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the ‘average’ species, which in this case only shows minor effects of the treatments. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site has support for multiple models and the posterior predictions were averaged across winning models: Removal + Warming, Removal, Removal × Warming, and Ambient. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species’ cover rather than inferred parameters.

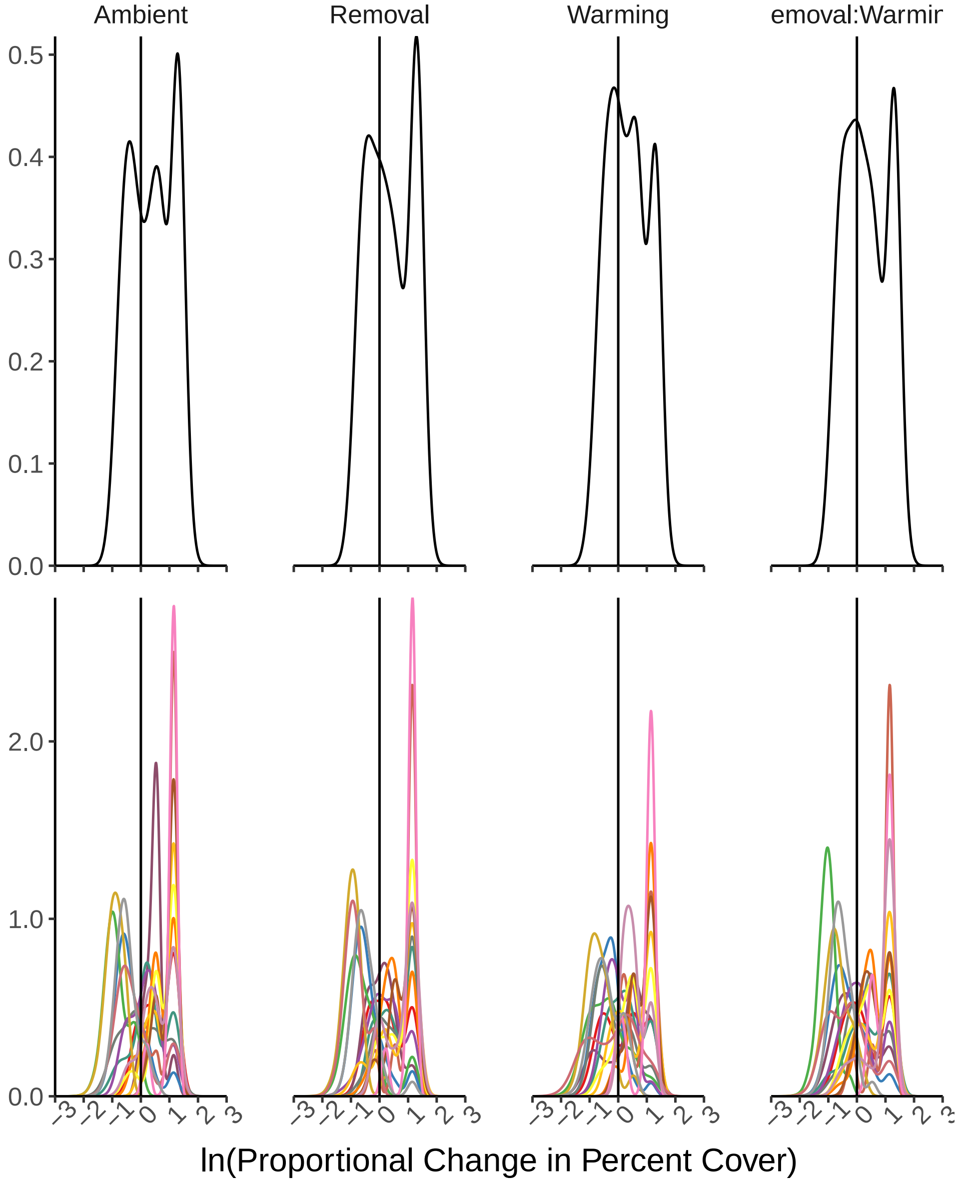

FIGURE A.8: Distribution of predicted change in percent cover within the high elevation Swiss site. Logarithmic proportional change in cover is calculated as ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}})$) as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. Treatment or combination models did not receive any model support at this site so their predictions reflect the ambient predictions. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

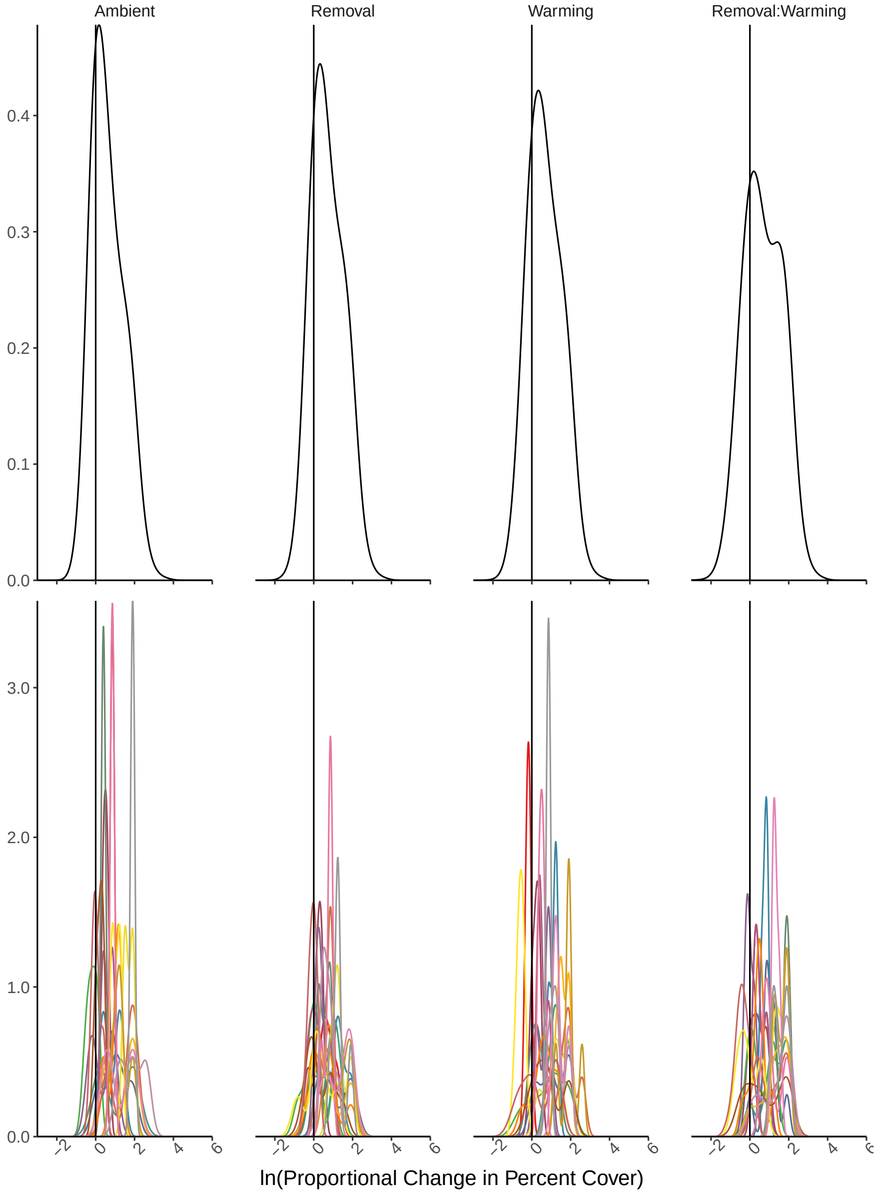

FIGURE A.9: Distribution of predicted change in percent cover within the low elevation China site. Logarithmic proportional change in cover is calculated as ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}})$) as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site showed support for multiple models and the posterior predictions were averaged across winning models: Ambient, Removal, and Warming. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

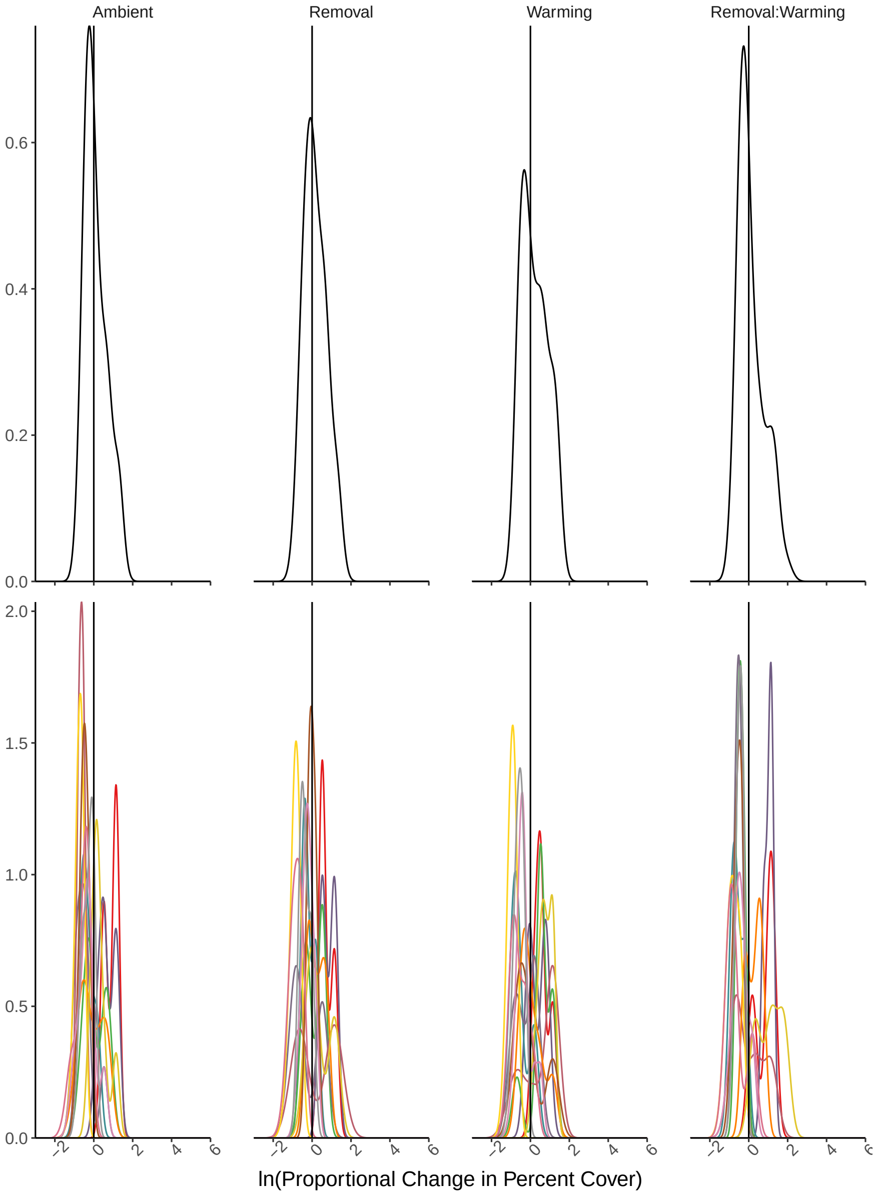

FIGURE A.10: Distribution of predicted change in percent cover within the low elevation New Zealand site. Logarithmic proportional change in cover is calculated as ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}})$) as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site showed some support for all treatment and interaction models and this figure reflects averaged parameter estimates.

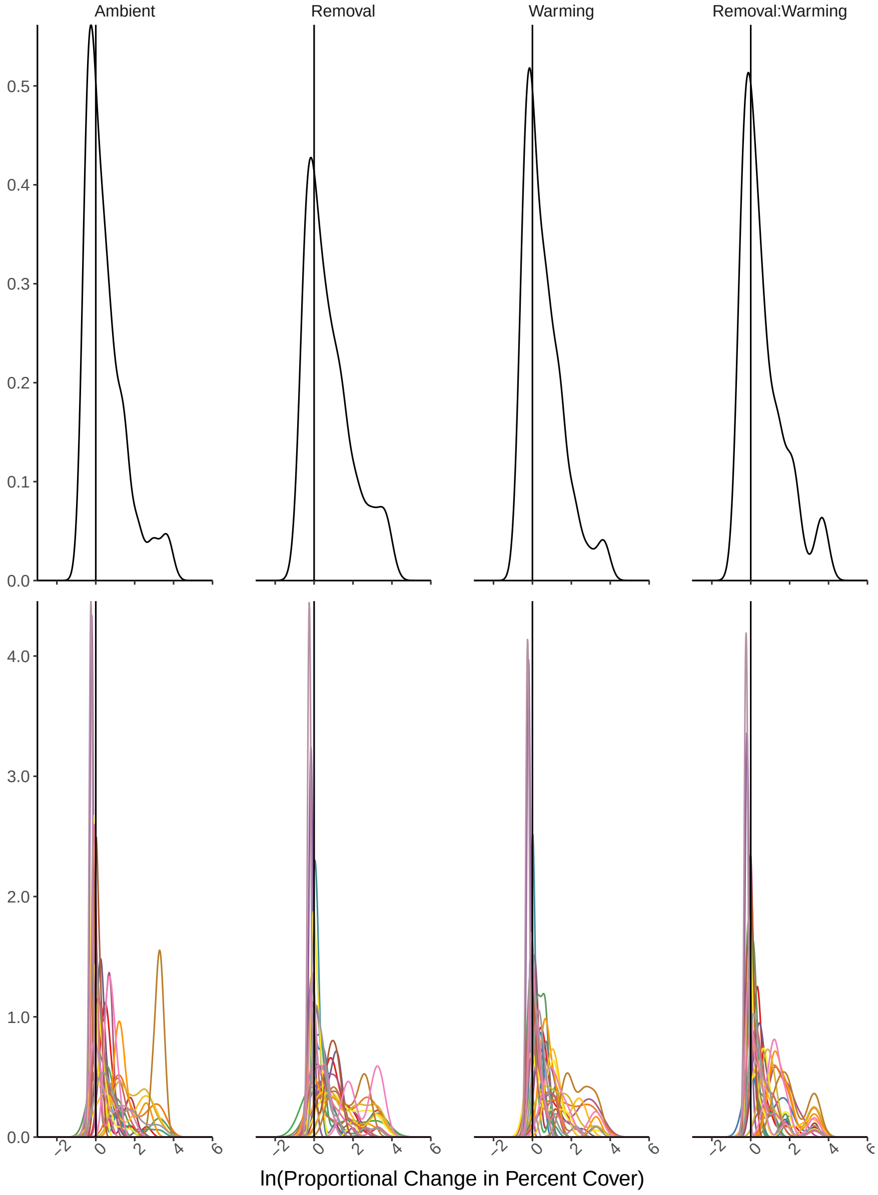

FIGURE A.11: Distribution of predicted change in percent cover within the low elevation New Zealand site. Logarithmic proportional change in cover is calculated as $(\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}}))$ as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero $(\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. Treatment models did not receive any model support at this site so their predictions reflect the ambient predictions. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

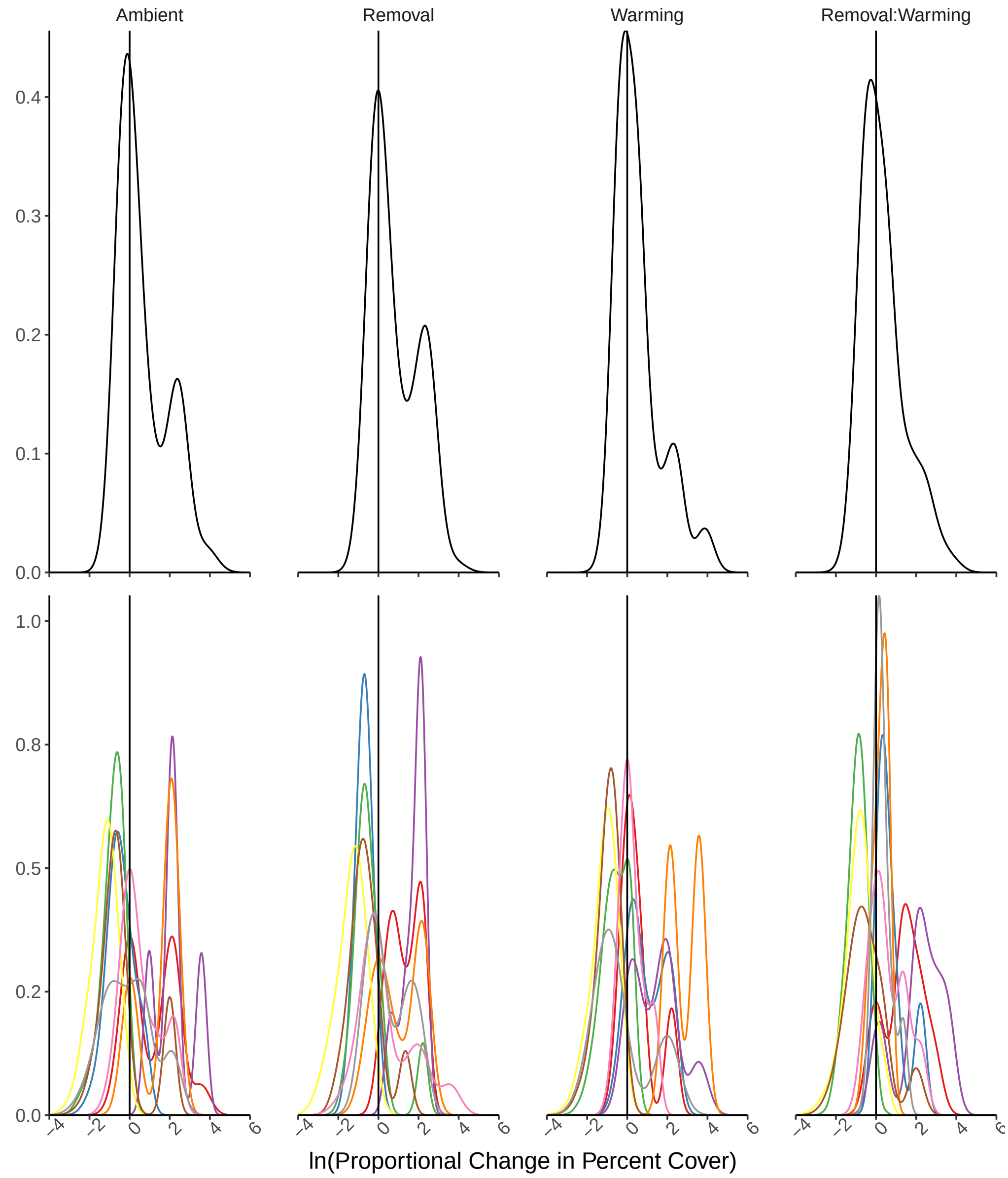

FIGURE A.12: Distribution of predicted change in percent cover within the high elevation New Zealand site. Logarithmic proportional change in cover is calculated as ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{G_{i|RW}})$) as sampled from the joint posterior for parameters in our statistical model. A logarithmic change of zero ($\ln(1) = 0$; solid vertical line) represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species, which in this case only shows minor effects of the removal treatment. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site showed support for multiple models and the posterior predictions were averaged across winning models: Removal × Warming, Warming, and Removal + Warming. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

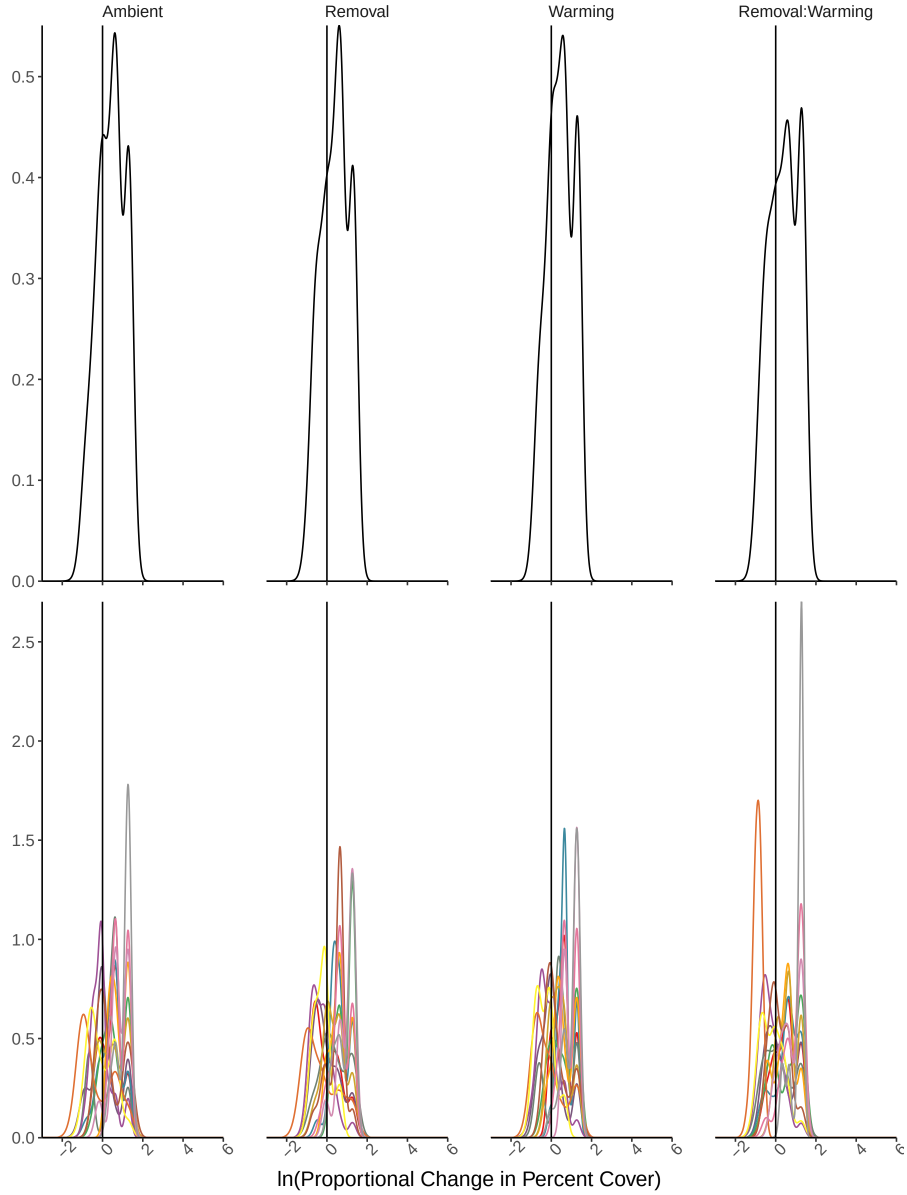

FIGURE A.13: Distribution of predicted change in percent cover within the low elevation United States site. Logarithmic proportional change in percent cover is calculated as a combination of density-independent and density-dependent factors $(\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{(}G_{i|RW}))$ is sampled from the posterior for each parameter in the model. A change in cover near zero represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. Treatment and combination models did not receive any model support at this site so their predictions reflect the ambient predictions. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

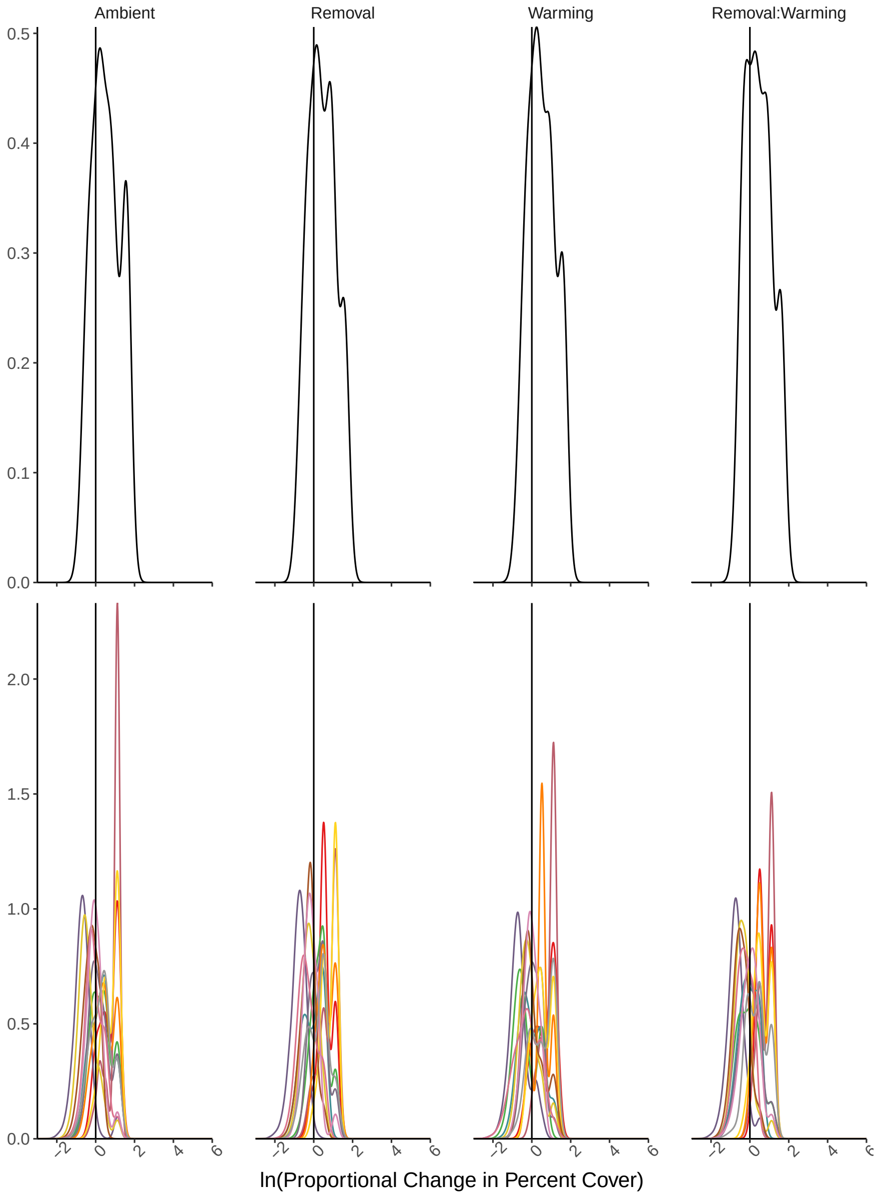

FIGURE A.14: Distribution of predicted change in percent cover within the high elevation United States site. Logarithmic proportional change in percent cover is calculated as a combination of density-independent and density-dependent factors ($\ln(N_{i,t}/N_{i,t-1}) = \ln(Q_i/N_{i,t-1} + e^{(}G_{i|RW}))$ is sampled from the posterior for each parameter in the model. A change in cover near zero represents no change over time suggesting that populations are at/near their equilibrium. The top row shows the predictions based on the community-level grand mean or the 'average' species, which in this case only shows minor effects of the warming treatment. The second row shows the predicted change in percent cover for all species at this site illustrating how species vary within and among treatments. This site showed support for multiple models and the posterior predictions were averaged across winning models: Warming, Ambient, and Removal + Warming. Since this metric includes observed previous cover, differences seen in unsupported treatments reflect variations in species' cover rather than inferred parameters.

Appendix B

Supplemental Material: Indirect interactions contribute to success of introduced annual plants

Methods

Field Methods

Seeds were collected from as many individuals as possible across all plots at the end of the field season when plants were near senescence. To ensure high seed retention, flowers/inflorescences were covered with mesh bags once the plants were no longer receptive to pollinators. Due to a short dispersal window and limited collection capacity, seed collection was not consistent across plots (seed collection ranged from 0.0% to 98.5%, with an average of 50%).

In some cases, plants matured over time and seeds were collected over multiple collection rounds with these rounds summed to a total fecundity of that individual plant to be used in analyses. Individuals where seeds were not collected were not included as focal individuals in the analyses. On the other hand, plants that never produced seeds (which is not to say those for which seed were not collected) were considered as potential focal individuals (with total fecundity = 0), and included in analyses because of the potential for strongly competing neighbors to completely suppress seed production.

Environmental parameters

At each plot, we took an image of the overhead canopy cover with a fisheye lens. We then calculated the percentage canopy cover using ImageJ (Rueden et al., 2017).

We also collected soil samples from each plot; we took a small sample from each side of the square plot and aggregated the small samples together to produce one sample for the plot. The samples were sieved (2.0 mm), sub-sampled (*c*. 5.0 g), and sent to the University of Queensland, School of Agriculture and Food Sciences Soil Testing Services for Colwell phosphorus analysis.

Soil water holding capacity was measured by taking 50g of dried soil (taken using the sampling method described above) and placing it in a filter. We then soaked the sample with water until saturated. We let the sample sit for 60 minutes (to let any excess water drip from the filter) and then we weighed the saturated sample. We then placed the samples in a drying over (60^oC)

for 2 weeks and re-weighed the dried samples. The difference in wet and dry weight divided by the dry weight results in percentage water holding capacity of the soil.

At each plot, we estimated percentage litter (from overhead trees and shrubs) as well as percentage bareground in the plot. We used percentage classes (1 through 6) to assess the litter and bareground: (1 = 1–5%, 2 = 6–15%, 3 = 16–25%, 4 = 26–40%, 5 = 41–60%, 6 = 60–100%). We took the mid-point of these classes to transform from a factor to a numeric percentage.

Summary of environmental parameters seen in Fig B.2.

Pantograph

The pantograph was designed to reduce the plot size to a 15 X 15 cm map, a 3:1 reduction. Each map was scanned using a high-resolution scanner (Doxie, 2016), cropped to 4400 x 4400 pixels^2 using a photo imaging software (GIMP; GIMP Development Team, 2016) and aligned so the north-most edge was at the top of the image. We then digitized the maps using geographic information systems (GIS) software (QGIS Development Team, 2016).

TABLE B.1: Names and abbreviations of focal species observed in this dataset. Species are classified into functional groups and life cycle. Species are refered to in figures by abbreviations. No. of Observations refers to the number of neighborhoods containing this focal.

Code	Species Name	Status	Functional Group	Life cycle	No. of Observations
ARCA	*Arctotheca calendula*	Introduced	forb	Annual	1029
CAHI	*Caltotis hispidula*	Native	forb	Annual	64
GITE	*Gilberta tenuifolia*	Native	forb	Annual	37
GOBE	*Goodenia berardiana*	Native	forb	Annual	80
GOPU	*Goodenia pusilliflora*	Native	forb	Annual	170
HYGL	*Hyalosperma glutinosum* subsp.*glutinosum*	Native	forb	Annual	139
HYPO	*Hypochaeris glabra*	Introduced	forb	Annual	50
MEDI	*Medicago* sp.	Introduced	forb	Annual	113
PEAI	*Pentameris airoides*	Introduced	grass	Annual	1040
PEDU	*Petrorhagia dubia*	Introduced	forb	Annual	39
PLDE	*Plantago debilis*	Native	forb	Annual	221
POCA	*Podolepis canescens*	Native	forb	Annual	529
POLE	*Podolepis lessonii*	Native	forb	Annual	86
PTGA	*Ptilotus gaudichaudii*	Native	forb	Annual	274
STPA	*Austrostipa elegantissima*	Native	grass	Perennial	107
TRCY	*Trachymene cyanopetala*	Native	forb	Annual	105
TROR	*Trachymene ornata*	Native	forb	Annual	43
VECY	*Velleia cycnopotamica*	Native	forb	Annual	79
VERO	*Velleia rosea*	Native	forb	Annual	1158
WAAC	*Waitzia acuminata*	Native	forb	Annual	137

Results

When fitting our generalized linear mixed effects models we used block as a random effect to account for variation in environmental parameters. The effect of block was generally centered

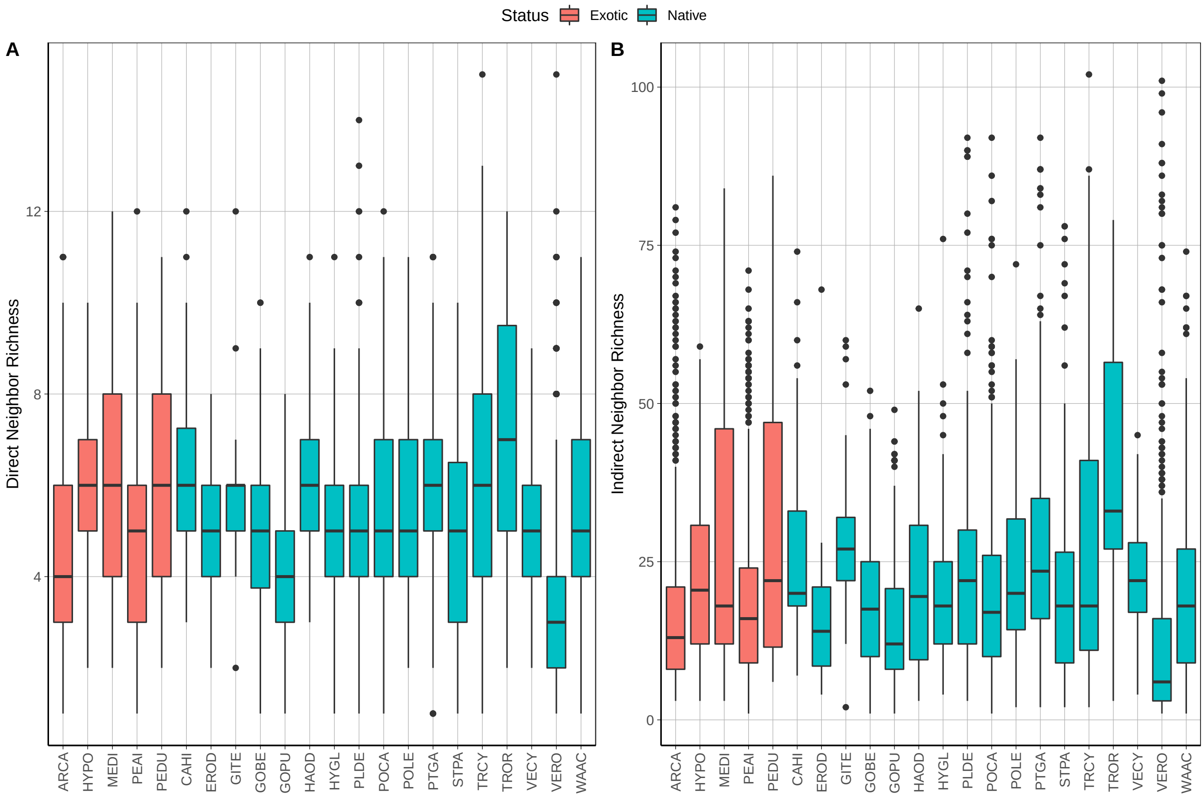

FIGURE B.1: Variation in richness of neighborhoods experienced by each focal. A) Direct neighbor richness each focal experienced. B) Indirect neighbor richness each focal experienced. Richness of both types of neighborhoods largely did not vary between focals or systematically between native or exotic focals.

around zero (ranging from -1.5 to 1.6) with the exception of *Hypochaeris glabra* which showed a strong effect of block (ranging from -27 to 13). The effects were similar in magnitude across native and introduced focal species (with the exception of *H. glabra*) and across the blocks (Fig B.3).

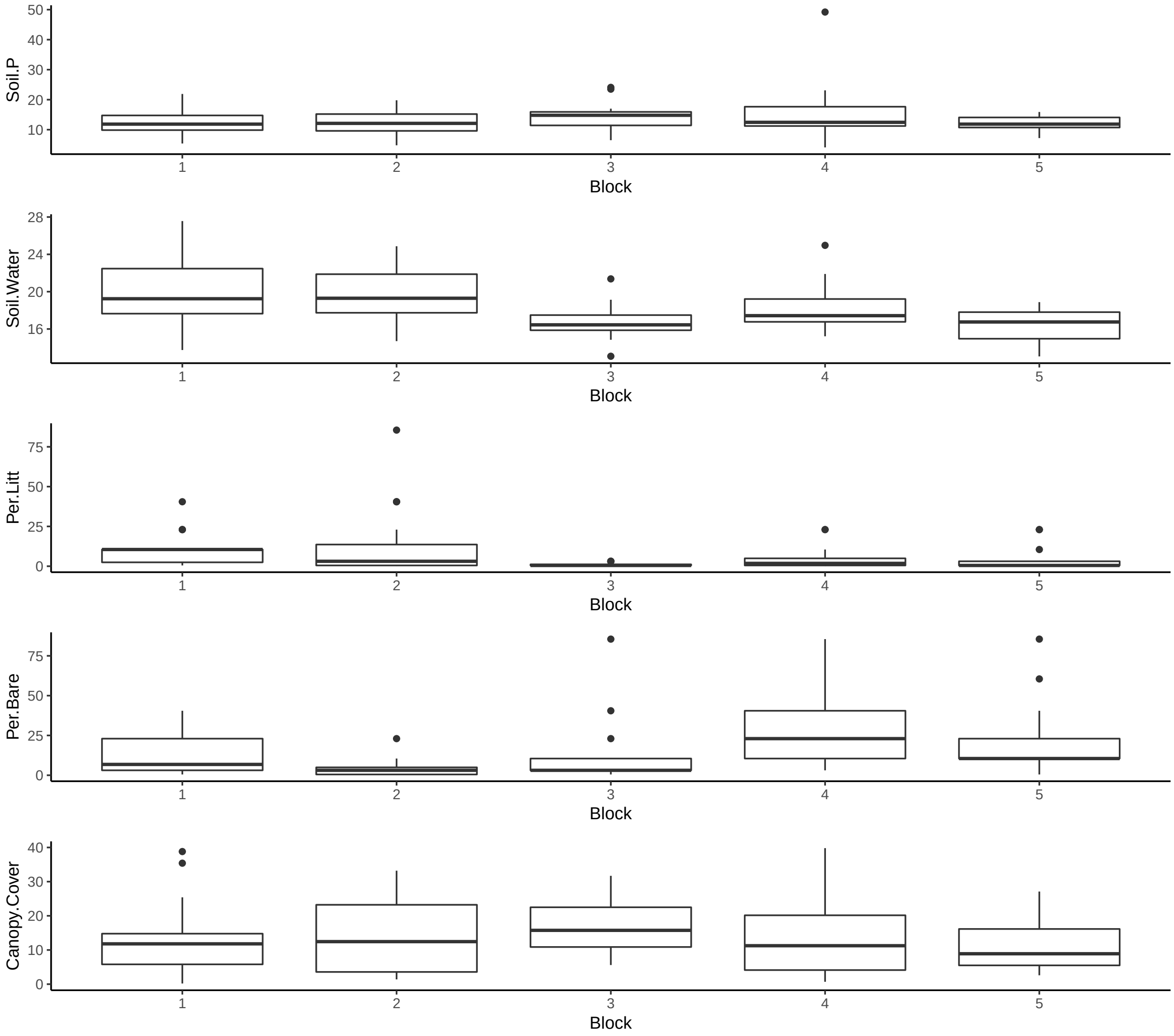

FIGURE B.2: Environmental parameters measured across this field study. Blocks were spaced across presumed environmental gradient. While parameters were measured on a plot level, we pooled these to examined the variation across blocks.

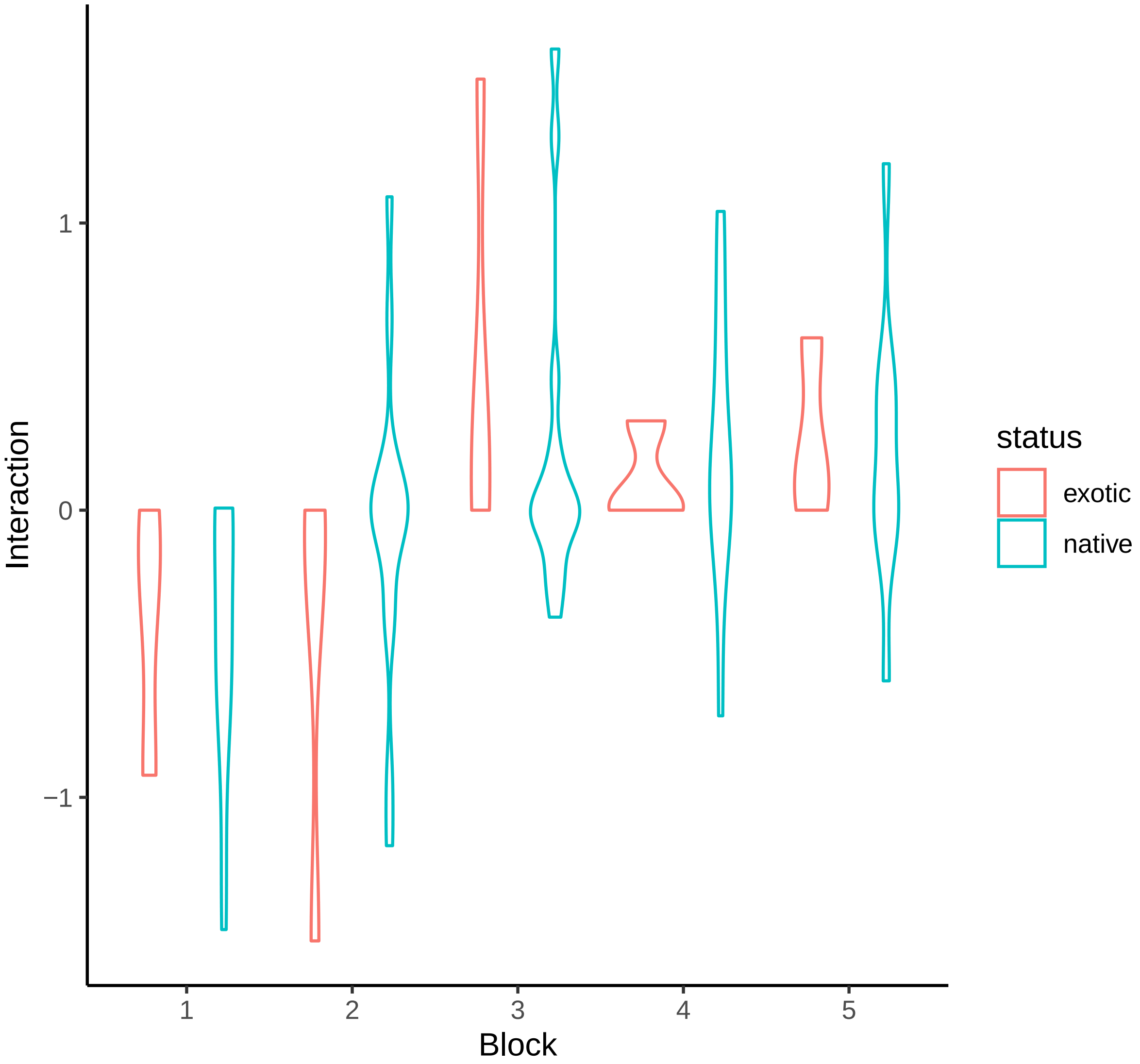

FIGURE B.3: Variability in the intercept associated with the random effect of block. Summarized for all focal species except HYPO. HYPO showed the greatest variability ranging from -27 to 13 while the remaining species centered around zero.

Appendix C

Supplemental Material: Interactions and life-history trade-offs govern persistence in space-limited benthic communities

Field Methods

Individuals from each species varied in size due to differences in growth form, but were randomly distributed among different tiles to avoid bias because of this variation. Hard-bodied organisms were attached to PVC tiles with marine epoxy (Water Weld JB weld and 3M marine sealant) and soft-bodied organisms were tied to tiles with dental floss. Most organisms grew over their attachment mechanism and no losses were evident after the first sampling period.

Owing to loss of organisms in the first 3 days after deployment, species richness of the experimental communities varied from one to eight species at the onset of the experiment and accumulated individuals and/or species overtime. This resulted in a total of 21 sessile invertebrate species being identified over the course of the experiment.

Bayesian Model Fitting

Our Bayesian, hierarchical model for our dynamic model of variation in percent cover of a focal functional group i within a sampled plot may be written as:

$$
\begin{aligned}
N_{i,t+1} &\sim \text{Beta}(\gamma_{i,t}, z, \phi) && \text{(C.1)}\\
\lambda_{i,t} &\sim Q_i + N_{i,t} e^{G_{i|C}} && \text{(C.2)}\\
Q_i &\sim \frac{0.5}{1 + e^{-(q+\Delta q_i)}} && \text{(C.3)}\\
G_{i|C} &\sim (\lambda + \Delta\lambda_i) - \sum_{j=1}^{c} (\alpha_{\cdot j} + \Delta\alpha_{ij}) N_{j,t} && \text{(C.4)}\\
\{q\} &\sim \text{Normal}(0, 5) && \text{(C.5)}\\
\{\Delta q_i, \Delta\alpha_{ij}\} &\sim \text{Multivariate normal}(\sigma, \rho) && \text{(C.6)}
\end{aligned}
$$

$$\sigma \sim \text{HalfCauchy}(0,2) \tag{C.7}$$

$$\rho \sim \text{LKJcorr}(1) \tag{C.8}$$

$$\phi \sim \text{Gamma}(0.01,0.01) \tag{C.9}$$

$$z_i \sim \text{Beta}(1,1) \tag{C.10}$$

where $\lambda_{i,t}$ refers to the mean predicted cover of functional group i in time point t.

A stationary chain shows a path that stays within the posterior distribution, close to a central tendency for the length of the chain (McElreath, 2016). A well-mixed chain means that each successive sample is not correlated with the previous sample, leading to a rapid zig-zag pattern (McElreath, 2016) whereas the Gelman-Rubin convergence diagnostic (Rhat) far above one generally indicates that a chain has not converged (Gelman and Rubin, 1992; Brooks and Gelman, 1998). The Cauchy distribution is a thick-tailed probability distribution; in this case, a half-Cauchy (restricted to positive values) acts as a weakly informative/regularizing prior for standard deviations (McElreath, 2016). The LJKcorr distribution of correlation coefficients provides a weakly informative prior on the covariance matrix which is skeptical of extreme correlations near -1 or 1 (Lewandowski et al., 2009).

Results

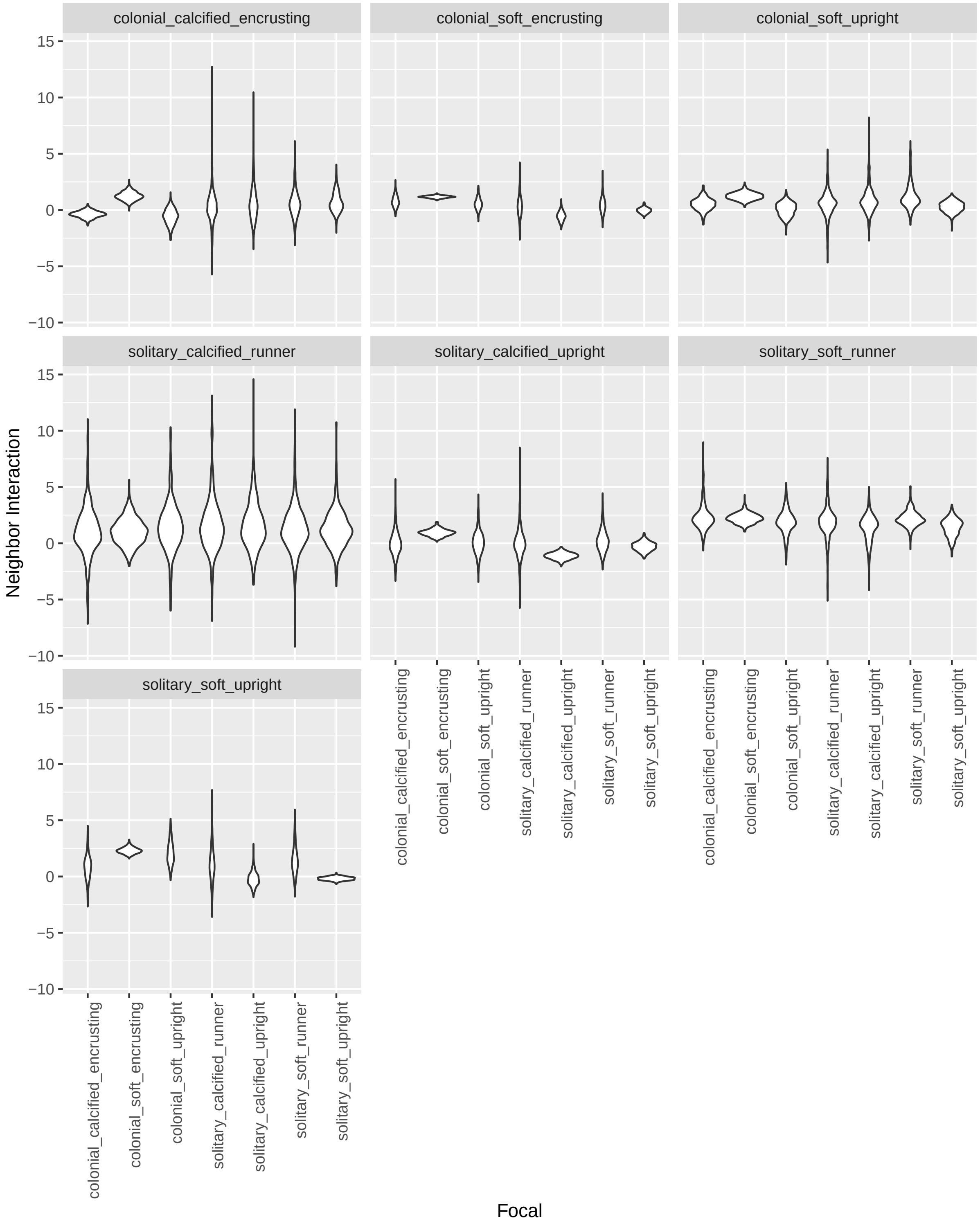

FIGURE C.1: Posterior draws of interactions between each focal functional group and neighbor. Each panel is a focal functional group, while the x-axis displays neighbors. Y axis shows the posterior estimates of interactions with each neighbor. Here competition is represented by positive coefficients and facilitation by negative coefficients. Shows the range of interactions based on 1000 posterior draws.

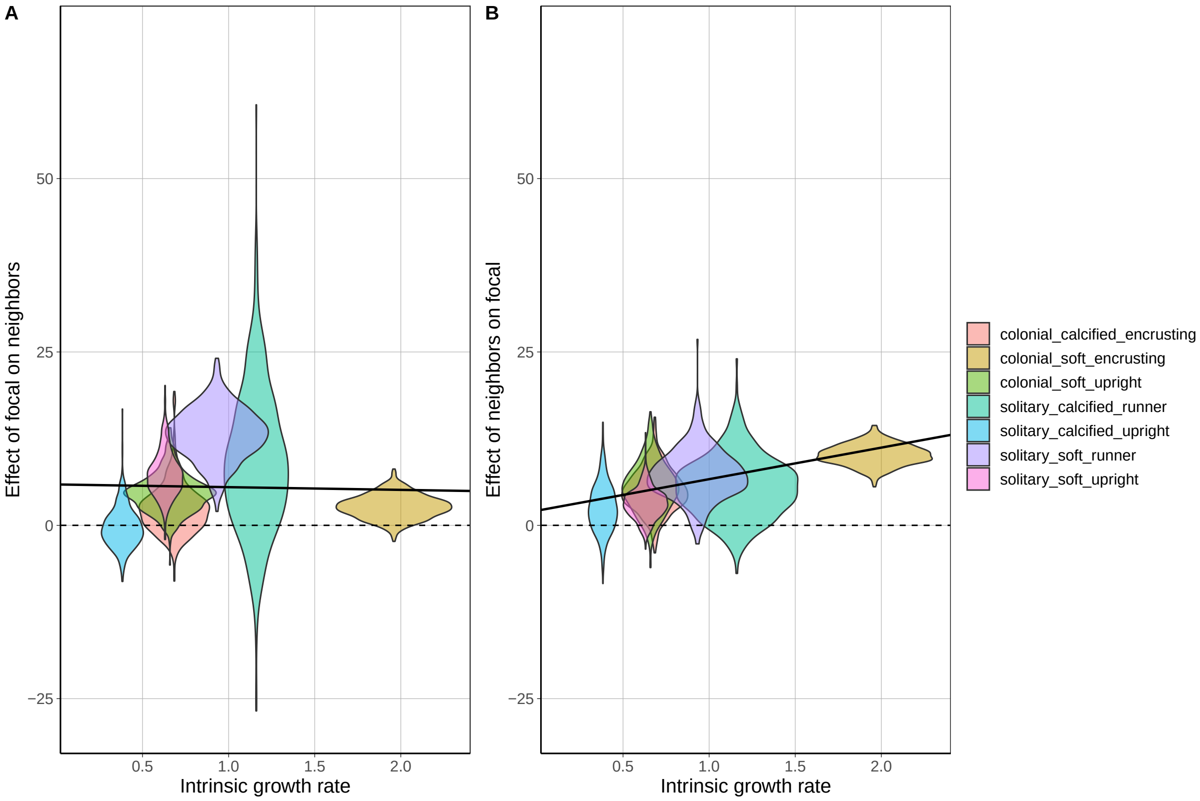

FIGURE C.2: Competition-growth trade-off of functional groups studied. Here growth refers to intrinsic or density-independent growth A) Relationship between inferred intrinsic growth (λ_i) and inferred competitive effects of a focal functional group on neighbors as the column sums of our inferred pairwise interaction matrix (community response, α_{ij}). Here we saw no trend between intrinsic growth and inferred competitive effects. B) How a group responds to the community, relationship between inferred intrinsic growth (λ_i) and the effect of neighbors on a focal functional group as the row sums of our inferred pairwise interaction matrix (community effects, α_{ji}). As intrinsic growth rate increases competitive interactions a group received increases. Competition is represented by positive coefficients and facilitation by negative coefficients. Based on 1000 posterior draws of each parameter.

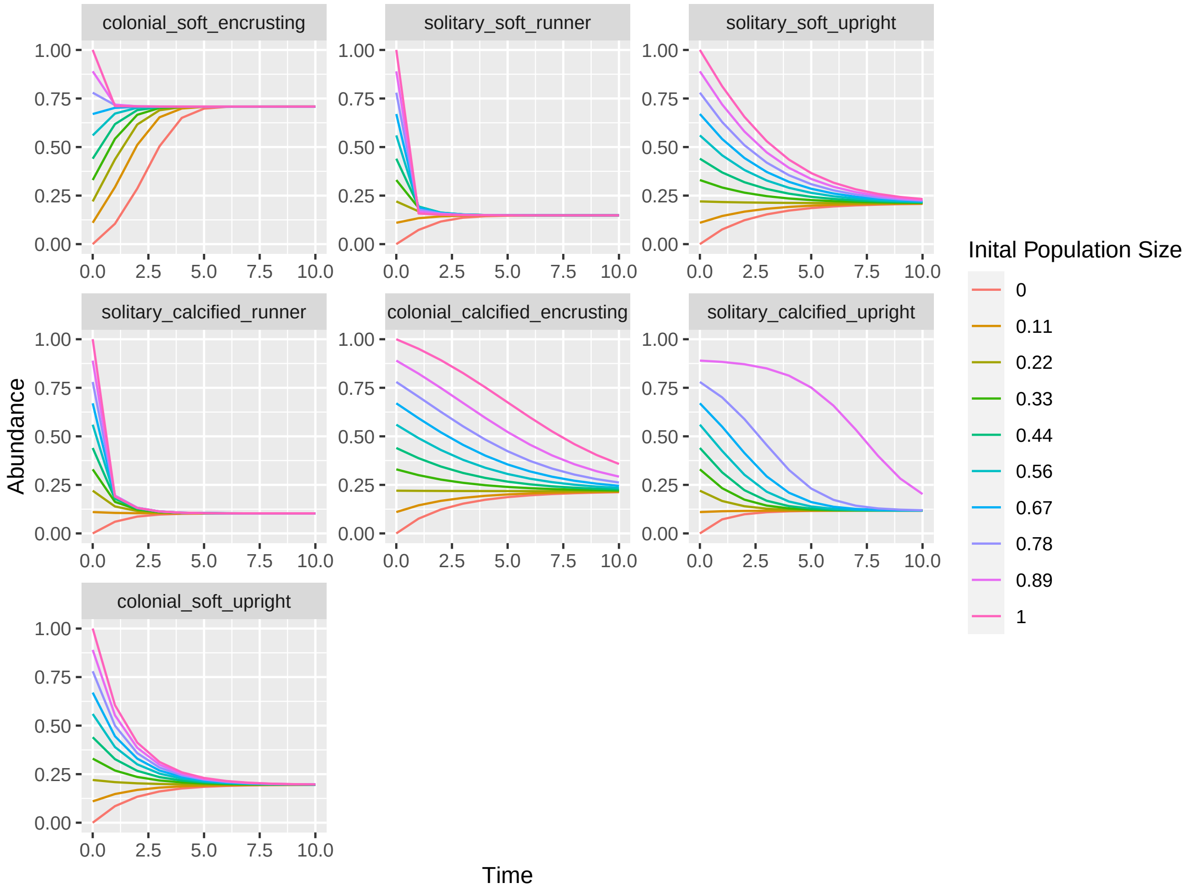

FIGURE C.3: Simulations of all seven functional group abundances over time in monoculture. Populations were started at ten abundances uniformly ranging from 0 to 1 and inferred median values were used for the remaining population dynamics parameters. Simulations were run for ten time steps where each time step represents two weeks. Solitary calcified upright group, with an initial population size of one is removed from this figure as it reached unrealistic population abundance (> 1).

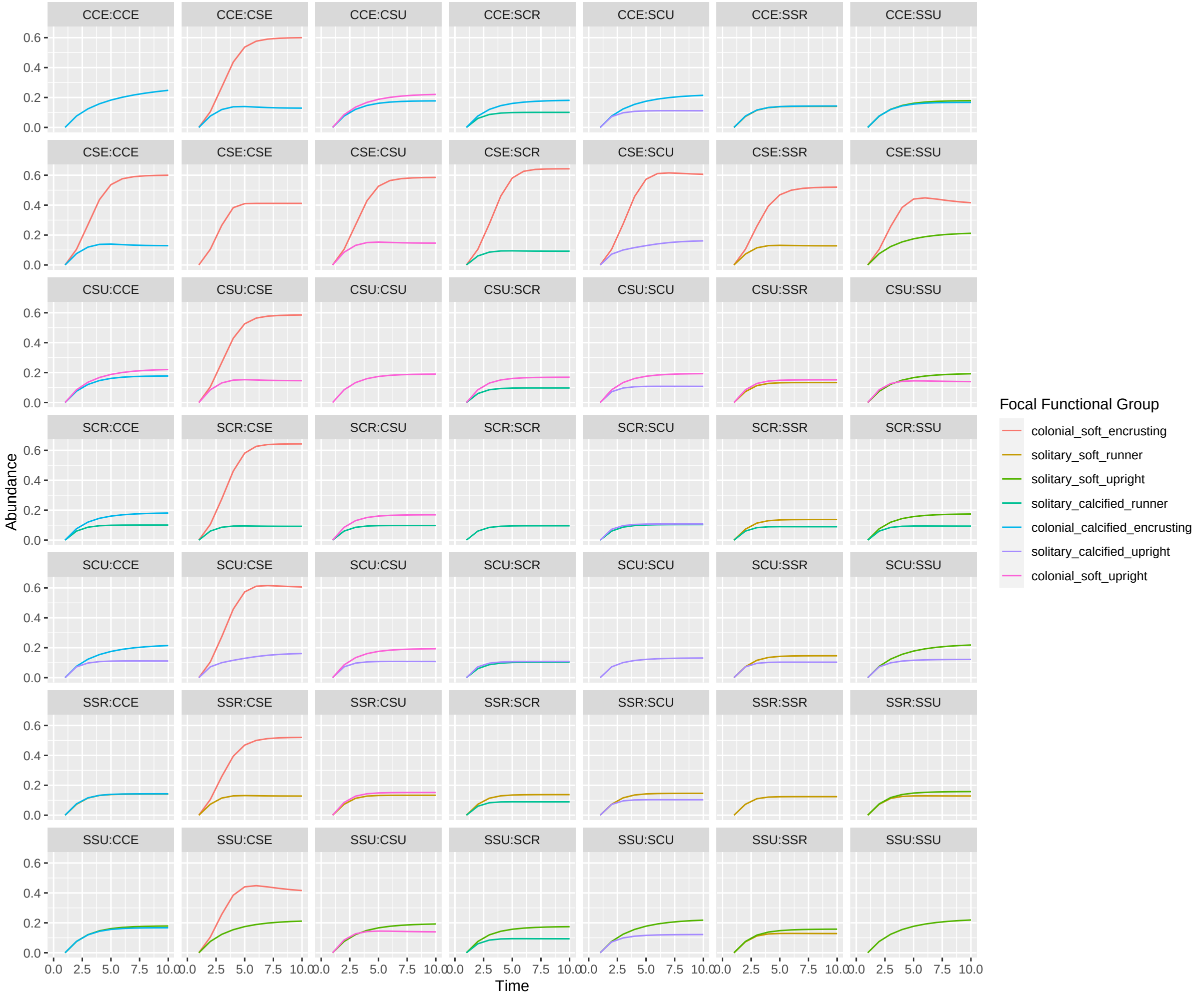

FIGURE C.4: Simulations of all pairwise competitions among functional group abundances over time. Diagonal shows monoculture interactions. Populations were both started at zero abundance and inferred median values were used for all remaining population dynamics parameters. Simulations were run for ten time steps where each time step represents two weeks.

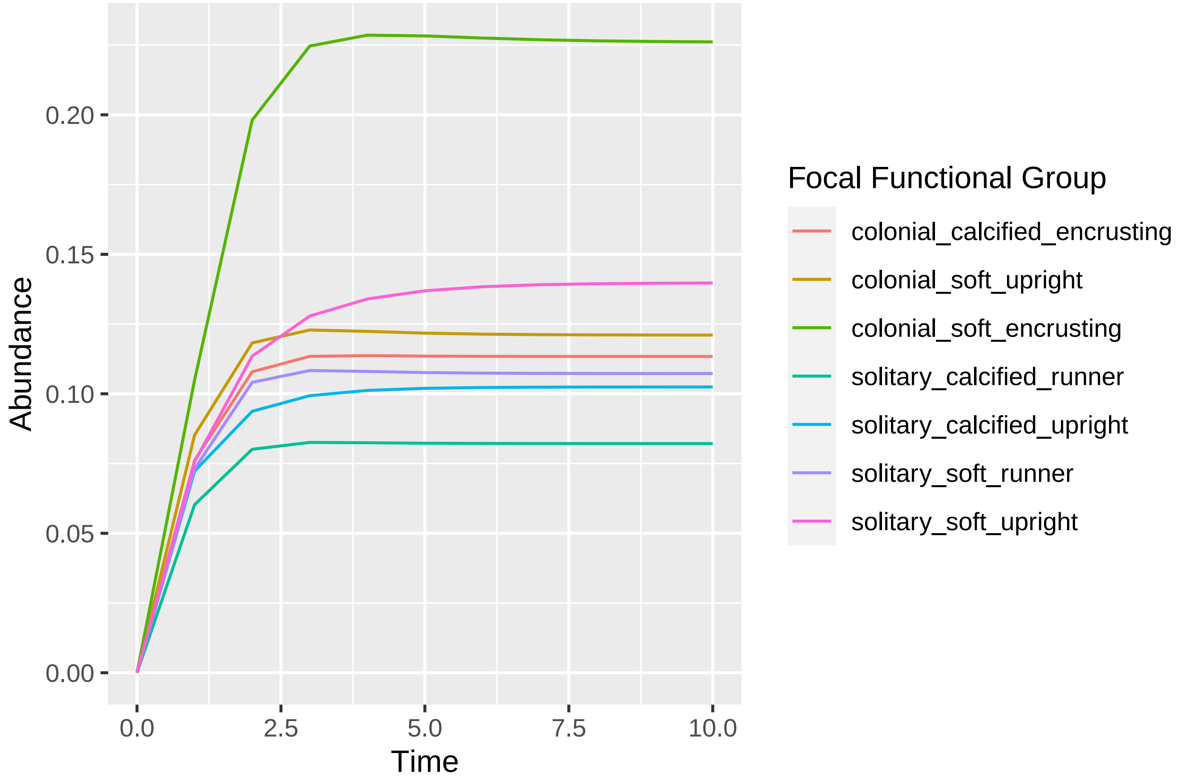

FIGURE C.5: Simulations of all seven functional group abundances over time in polyculture. Populations were both started at zero abundance and inferred median values were used for all remaining population dynamics parameters. Simulations were run for ten time steps where each time step represents two weeks.

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