Title

Mechanisms for Species Coexistence under Environmental Change: Insights from a California Grassland

Permalink

https://escholarship.org/uc/item/8vn5b96d

Author

Larios, Loralee

Publication Date

2013

Mechanisms for Species Coexistence under Environmental Change: Insights from a California Grassland

By

Loralee Larios

A dissertation submitted in partial satisfaction of the requirement for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Katharine N. Suding, chair
Professor James W. Bartolome
Professor Wayne P. Sousa

Fall 2013

ABSTRACT

Mechanisms for Species Coexistence under Environmental Change: Insights from a California Grassland

By

Loralee Larios

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor Katharine N. Suding, Chair

Understanding the potential mechanisms that influence invasion resistance and coexistence in plant communities has been a central tenet of invasion ecological research during the past few decades. My dissertation used observational and experimental approaches to understand what processes influence whether a community is invaded, resists invasion, or results in species coexistence within a California grassland. Chapter 2 reviewed the impacts that alien plant species may have on communities and provided a framework for how to identify when invader impacts lead to recovery constraints for the native community and integrate these constraints into restoration efforts. Chapter 3 investigated how species effects on resource availability can result in differing invasion dynamics in native versus exotic dominated grasslands. I found that while exotic and native species differentially alter the availability of light and nitrogen in a community, nitrogen availability is key in determining invasion of an exotic into a native grassland as well as the invasion of a native into an exotic dominated community. Chapter 4 investigated how propagule pressure after an extreme disturbance can result in the invasion of intact native grasslands. I found that the recovery of native grassland stands after an extreme disturbance (fire+drought) can be stalled by an influx of exotic propagules from the surrounding matrix. Chapter 5 addressed how the strength of plant-soil feedbacks for a native and exotic may change with soil resource availability changes on soil communities and with a competitor. I found a negative effect of exotic conditioned soil on native growth and no effect of native conditioned soil on exotic growth, suggesting that plant-soil feedbacks may facilitate the establishment of the exotic as well as its dominance. Lastly, Chapter 6 investigated how seed addition and soil amendments management efforts affected native recovery after an extreme disturbance. I found that seed additions and soil N reductions were able to increase the establishment and fitness of some natives, but may not be sufficient to promote full native recovery. This work provides a tool to understand not only why native resident communities are invaded but also how to reduce the resistance of invaded communities and increase the resistance of native communities. Additionally this work allowed me to integrate the impacts that exotic species have on communities to make general predictions about the recovery of native communities after an extreme disturbance or control efforts. Overall, I observed that native communities and populations are vulnerable to invasion after a large disturbance and with nitrogen enrichment. From low to moderate nitrogen availability, native and exotic species should coexist due to niche partitioning, but not as a result of density dependent negative plant-soil feedbacks. Lastly, I found that an exotic species is able to maintain its dominance due to its strong competitive effect on native species, particularly at high nitrogen availability and its ability to culture a soil community that negatively impacts the growth of native species.

DEDICATION

I would like to dedicate this dissertation to my parents, Pablo and Sylvia Larios, who have overcome many obstacles to provide me with this opportunity and who have supported me in all of my endeavors.

I would also like to dedicate this dissertation to my partner, Marko Spasojevic, who supported me unconditionally throughout this process and believed in me when I could not.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

I am indebted to many people for their help with my dissertation, and I will try to thank as many as I can, but please forgive me if I forget anyone.

I would like to start by thanking my mentor and advisor, Katharine Suding. Her guidance, patience, and demand for excellence over these past few years have helped me push my limits and accomplish all that I have professionally and scientifically. I would also like to thank my committee James Bartolome and Wayne Sousa for their guidance and input.

Working on a dissertation can be a long exhausting journey, but I was very fortunate to have amazing labmates in the Suding lab, who provided me help, comfort, and laughs over the years. As such, I would like to acknowledge lab members past and current, who were such a pleasure to work with: Dr. Stan Harpole, Dr. Dan Potts, Dr. Isabel Ashton, Dr. Rebecca Aicher, Dr. Leah Goldstein, Dr. Heather McGray, Dr. Marko Spasojevic, Dr. Rebecca Shirk, William Schlegel, Michelle Chang, Diana Hsueh, Margaret Royall, Jane Smith, Charlotte Riggs, Warren Sconiers, Chris Kopp, Dr. Claudia Stein, Dr. Susana Rodriguez-Buritica, Dr. Brad Butterfiled, Dr. Laura Yahdjian, Dr. Emily Farrer, Lauren Hallett, Joanna Hsu, Dr. Erica Spotswood and Liana Nichols. I would also like to thank the UC Berkeley range group who welcomed me to all their lab meetings and provided me with great insights into California grasslands

I would like to thank the South Coast Research and Extension Center for providing the space for part of my dissertation work. I would like to give a special "Thank you" to Joanne Watkins for all her help and for humoring all of our sampling ideas no matter who silly they may have been. Thank you to the Irvine Ranch Conservancy for providing access to research sites for a major part of this dissertation. Much of this work was made possible by generous funding from the NSF Graduate Research Fellowship Program and NSF DEB 09-19569. I would like to additionally thank S&S Seeds for donating seeds for some of this work and Zadro, Inc for providing the mirrors for my light manipulations.

I have many people – undergrads, fellow graduate students, and family alike – to thank for all their time in the field or lab, counting and sorting plant parts: Alexandra Chou, Rebecca Aicher, Rawan Almomani, Lisa August-Schmidt, Elizabeth Baker, Hortencia Bueno, Jennifer Butler, Bardo Castro, Nick Cash, James Chan, Hong Chen, Alexandra Chou, Truc Dinh, Tammy Dong, Joanna Fong, Hui Gao, Leonardo Larios, Pablo Larios, Sylvia Larios, Mitchell Luu, Julian Martinez, Heather McGray, Liana Nichols, Emma Nilsson, Rachel Phoa, Christie Shiang, Emily Stone, Quinn Sorenson, Rebecca Shirk, Marko Spasojevic, Zoe Statman-Weil, Natalie Tan, Stephanie Tiang, Tracy Popiel, Jennifer Weber, Bailey Wilson, Daniel Yoo, and Jesse Zablan.

Thank you to Tracy Popiel and Katherine Diaz for many years of support and friendship. Tracy, thank you for helping me with fieldwork on your days off, and Kat, thank you for never letting me lose sight of my goal.

I have made some wonderful friends through this process: Rebecca Aicher, Kristina Cervantes-Yoshida, Lauren Hallett, Heather McGray, Erica Spotswood, Jenny Talbot, and many more. Thank you all for all the great times.

Lastly, I would like to thank my partner and my family. Marko, thank you for your constant words of encouragement; you have been my rock through this whole process.

Mom and Dad, thank you for teaching me the value of hard work and diligence and for supporting me through this dissertation even when it meant that I would have to move away and you would have to be clipping plants on your days off. Pablo, thank you for helping me embrace my nerdiness, and Leo, I've been dragging you out to the field since you were 11; thank you for keeping me company all of these years.

CURRICULUM VITAE

Loralee Larios
Environmental Science, Policy and Management
University of California-Berkeley
137 Mulford Hall #3114
Berkeley CA 94720
Email: LLarios@berkeley.edu

Education

2009-present	PhD Candidate, University of California at Berkeley, Department of Environmental Science, Policy and Management
2007-2009	University of California at Irvine, Department of Ecology and Evolutionary Biology, PhD program (transferred to UC Berkeley before completion)
2000-2005	California State University, Fullerton, Bachelor of Science (*magna cum laude*) in Biology

Research Interests

Plant community ecology, restoration ecology, invasion ecology, plant-animal interactions, human impacts on ecosystems, threshold dynamics and plant-soil feedbacks

Appointments

2013	Graduate Student Researcher, University of California, Berkeley
2011-2012	Graduate Student Instructor, University of California, Berkeley
2011	Graduate Student Researcher, University of California, Berkeley
2008	Graduate Research Assistant, University of California, Irvine
2007-2008	Graduate Teaching Assistant, University of California, Irvine
2005-2007	Lab Manager/Research Technician. University of California, Irvine
2004-2005	Student Researcher. California State University, Fullerton
2004-2005	Naturalist. Tucker Wildlife Sanctuary. Modjeska Canyon, CA.
2003-2004	Student Researcher. California State University, Fullerton

Publications

Larios, L., R.J. Aicher, and K.N. Suding. *In press.* Effect of propagule pressure on recovery of a California grasslands after an extreme disturbance. Journal of Vegetation Science. DOI: 10.1111/jvs.12039.

Larios, L. and K.N. Suding. *In press.* Restoration within protected areas: when and how to intervene after plant invasions? In: Foxcroft, L.C., Richardson, D.M., Pyšek, P. and Genovesi (eds). *Alien Plant Invasions in Protected Areas.*

Cleland, E., **L. Larios**, and K.N. Suding. 2012. Strengthening invasion filters to re-assemble native plant communities: soil resources and plant phenology. Restoration Ecology 21: 390-398.

Aicher, R., **L. Larios**, and K.N. Suding. 2011. Seed supply, recruitment and assembly: quantifying relative seed and establishment limitation in a plant community context. The American Naturalist 178:464-477.

Larios, L. and P. Stapp. 2006. Effects of invasive thistle on grassland arthropod communities. CSUF Dimensions 8: 37-44.

Presentations

Larios, L. and K.N. Suding. 2013. Unraveling when elevated nitrogen conditions will result in plant invasions. [Presentation] Ecological Society of America. Minneapolis, MN

Stein, C., Farrer, E., **Larios, L.**, and K.N. Suding. 2013 A new era of keeping up with the joneses: why neighbors matter to environmental change. [Presentation] ESPM Departmental Seminar (Distinguished ESPM Research Group-Presentation)

Larios, L. and K.N. Suding. 2011. Natural disturbances affect invasion resistance in a California Grassland. [Poster] SACNAS, San Jose, CA

Larios, L. and K.N. Suding. 2010. Natural disturbances affect community trajectories within a California grassland. [Presentation] Ecological Society of America. Pittsburgh, PA.

Larios, L., M. Chang, and K.N. Suding. 2008. Resistance isn't futile: native grasslands persist in the midst of invasion [Poster] Ecological Society of America, Milwaukee, WI

Suding, K.N., E. Cleland, and **L. Larios.** 2007. Restoring by reassembly: Functional trait and resource controls on invasion. [Presentation] Ecological Society of America. San Jose, CA.

Larios, L. & Keber R. 2003. Effects of topography and vegetation on wild artichoke. [Poster] Annual Meeting of Sigma Xi. Los Angeles, CA

Awards

2013-2016 National Science Foundation Postdoctoral Research Fellowship in Biology
2008-2013 National Science Foundation Graduate Research Fellowship
2010 ESA Strategies for Ecology Education, Development, & Sustainability (SEEDS) alumni annual meeting travel award
2010 Department of Environmental Science, Policy & Management Travel Funds
2008 Biological Sciences Dean's Office Conference Travel Funds
2008 Department of Ecology and Evolutionary Biology's Conference Travel Funds
2007 Minority Biomedical Research Support Program (MBRS) Graduate Summer Fellowship
2002 – 2005 Southern California Ecosystem Research Program Scholarship
2004 ESA Strategies for Ecology Education, Development, & Sustainability (SEEDS) Student Travel Fellowship
2000 – 2004 President's Scholarship, CSUF (academic)
2003 Excellent Poster Presentation, Sigma Xi

Departmental Service

Student representation, ESPM Landscape Ecologist Faculty Search Committee, Dec 2012-May 2013

Student representative, ESPM-Graduate Programs Committee, Aug 2012-May 2013.

Student member, Teaching Seminar, Fall 2012. Redesigned teaching evaluations.

Student member, ESPM graduate student task force, Fall 2010. Task force for redesigning graduate student core courses

Secretary, ESPM Graduate Student Association, Sept 2009-May 2010

Professional Service

Reviewer: Biological Conservation (journal), Rangeland Ecology & Management (journal)

Synergistic/Volunteer Services

Coordinator, Diversity Roundtable Discussion at ESPM Graduate Student Conference, 2012
Co-Organizor, UCB ESA SEEDS chapter's Undergraduate mentoring program 2011, 2012.
Mentor, Environmental Leadership Pathways (ELP) student, Summer 2011
Planning committee, ESA SEEDS Western Leadership Meeting April 2010
Alumni Mentor for SEEDS, ESA Annual Conference, Pittsburgh, PA August 2010
Volunteer, Golden Gate Audubon Society's EcoOakland. Oct 2009-June 2010.
Mentor, UCB undergraduate interested in ecological research (Jennifer Butler Feb-May 2010; Elizabeth Baker, Hortencia Bueno, and Emily Stone Sept 2010-May 2011; Nina Algapcan and Stephanie Tang Sept 2011-Dec 2011; Alexandra Chau, Rachel Phoa, Victoria Le, and Bang Tran Jan-May 2012)
Mentor, UCI undergraduates interested in ecological research (Michelle Chang and Rawan Alwanadi Sept 2007-June2008; James Chan, Daniel Yoo, and Natalie Tan Sept 2008-June 2009)
Project Leader, Sage Hill School, Experiential Learning Program. 2006-2007.
ENLACE (ENgaging LAtino Communities for Education initiative) Student Affiliate. 2004-2005. Santa Ana Partnership.

Chapter 1

Introduction

Environmental changes – rising temperatures, changed precipitation patterns, increased atmospheric deposition – are affecting ecosystems at an unprecedented scale and pace (Luque et al. 2013). A critical challenge is to understand and predict how these global changes affect the interactions that mediate ecological diversity (Suding et al. 2008, Tylianakis et al. 2008). This challenge is further complicated by the fact that plant communities are often responding to multiple drivers of global change (Templer and Reinmann 2011). In light of potential synergistic interactions among global change drivers, there has been a renewed interest in using a more holistic system approach to not only predict how ecological systems may change but to inform management and restoration practices (Evans et al. 2012, James et al. 2013). My dissertation work was aimed at identifying such potential synergistic interactions among environmental change factors to predict future invasions and guide restoration efforts.

In my dissertation, I have applied a holistic approach to the issue of invasion in California grasslands. I build a framework that takes into account how exogenous drivers (fire and drought disturbance, atmospheric nitrogen deposition) influence neighborhood type and soil resources and the consequences of these controls on processes such as competition and plant-soil interactions and their ultimate impact on invasion (Figure 1). In this introductory chapter, I present a brief overview of my study system, then the rationale and overview of this framework, and highlight how my research sits within this framework.

Study System. California grasslands are an excellent system in which to explore invasion dynamics. It is estimated that over 9.2 million hectares of native perennial grasslands have been converted to exotic annual grasslands due to overgrazing and drought in the 1800s (Jackson 1985). Native grasslands have still not recovered, even when grazing has been removed (Stromberg and Griffin 1996); however, there are areas where native species have been able to persist (Stromberg and Griffin 1996, Gelbard and Harrison 2003). Studies in California grasslands suggest that competitive rankings between exotic and native grasses often vary depending on initial conditions (Dyer and Rice 1999, Hamilton et al. 1999, Lulow 2006, Abraham et al. 2009), indicating that frequency-dependent fitness differences (priority effects) may play a role in invasion resistance of both exotic and native grasslands. Other studies have found evidence for niche partitioning mechanisms promoting coexistence (Harpole and Suding 2007) and fitness differences (Seabloom et al. 2003b). However, few studies have simultaneously investigated fitness differences resulting in either invasion or invasion resistance, and how these may depend on positive feedbacks. Even fewer still have addressed how these processes change along resource gradients, a critical component of assessing invasion resistance (but see Corbin and D'Antonio 2004a, Thomsen and D'Antonio 2007). Furthermore, southern California is predicted to experience more severe droughts (Bell et al. 2004, Hayhoe et al. 2004) and is already experiencing altered fire regimes (Syphard et al. 2007) and high rates of nitrogen deposition (Fenn et al 2003) due to increased human activity. Understanding how native grasslands respond to these combined disturbances will be important to their future management and conservation.

Invasion in a community context. During the past few decades, ecologists have recognized the ability of invasive exotic species to alter ecosystem function, biodiversity, and disturbance regimes (Vitousek et al. 1997b, Mack et al. 2001, Levine et al. 2003). Because of the large impact that invasive species can exert on ecosystems, much research has been spent on identifying potential traits of successful invaders (Baker 1965, Rejmanek and Richardson 1996, Milbau and Nijs 2004), as well as identifying characteristics of sites resistant to invasion (Crawley 1987). The latter is important to understand as land managers try to impede exotic invasions by managing for resistance (D'Antonio et al. 2001). While the distinction has been useful (e.g., Fargione and Tilman 2005, Thomsen and D'Antonio 2007), both invasiveness and invasibility often emerge as weak predictors of success (Levine et al. 2004). In particular, these approaches of looking for predictive invader and habitat traits have limited applicability in assessing when exotic species may become naturalized (i.e., reach only moderate abundance, weakly impact) and when they may completely transform (i.e., reach high abundance, strongly impact) a plant community.

The prevalence of context-dependency – interactions among species traits and site characteristics – in invasions may require an alternate conceptual framework (Shea and Chesson 2002, Eppstein and Molofsky 2007). Chesson (2000) proposed that species coexistence results from a balancing of stabilizing processes (niche differences) and equalizing processes (average fitness differences), such that coexistence would occur if there was minimal niche overlap or when species' fitness were similar. Recently, MacDougall et al. (2009) incorporated this theory into invasion dynamics to show how leading invasion hypotheses, such as negative soil feedbacks (Bever et al. 1997) or enemy escape (Keane and Crawley 2002), all fundamentally relate to fitness differences (Figure 1 "Direct Controls"). Invasion resistance by the resident community would depend on high resident[1] fitness relative to invader fitness, while coexistence with the invader would result primarily from niche differences, when resources are limiting (MacDougall et al. 2009; Chapter 3).

Local scale interactions have been at the center of ecological research targeted at understanding not only plant community composition but also the establishment success of invaders (Figure 1, "Indirect Controls"). Competitive interactions have been used to explain both the success of an invader and the ability of a site to resist invasion depending on niche overlap between the invader and residents, where high niche overlap would reduce the invader's fitness relative to the resident resulting in invasion resistance (i.e. limiting similarity; Crawley 1987, Crawley et al. 1999). On the other hand, facilitative interactions often result in the successful establishment of an invader if the resident community is able to buffer the effect of other negative interactions (e.g., herbivores, pathogens; Cushman et al. 2011). In my work, I have found evidence of very strong

---

[1] I use *resident* to denote a species at relatively high abundance (regardless of whether it is of native or exotic origin) and *invader* to denote a species (or often in my experimental tests, an individual) that is entering the community at low abundance. Thus, invasion can be exotic individuals invading native resident communities, or vice versa.

competitive effects of the invader on native species, particularly at the seedling recruitment stage (Chapters 3, 4, & 5).

In addition to plant-plant interactions, plant-soil interactions also play an important role in an invader's establishment success at the local scale. Negative plant-soil interactions, where a species impacts the soil community in a way that decreases its fitness, are thought to result in species coexistence and be prevalent in native communities. Conversely, neutral to positive feedbacks can allow invaders to successful establish if the invader is not negatively affected by the resident soil community or able to alter the soil community as it increased in abundance to negatively affect the fitness of the residents, respectively (Wolfe and Klironomos 2005, Eppinga et al. 2006, Bever et al. 2010). Both of these mechanisms are likely operating simultaneously within a system, and teasing apart how these processes may interact is key to understanding which processes are more significant to invader establishment (Brandt and Seabloom 2012). I observed that the exotic, *Avena fatua* L., experienced neutral feedbacks when grown with native conditioned soil and that the exotic conditioned soil negatively affected the growth of the native *Stipa pulchra* Hitchc., both mechanisms likely contribute to the successful establishment of the exotic as well as their maintained dominance (Chapter 5).

This framework can be expanded to consider that a niche is not simply defined by species resource requirements but also by the effects that a species at high abundance has on resources or other trophic levels (Chase and Leibold 2003; Figure 1 "Interactive Controls"). For instance, at high abundance, a resident species can increase invasion resistance by reducing resource availability, altering rates of nutrient cycling, or influencing the soil microbial community in a way that enhances its fitness advantages over an invader (Tilman 1988, Chesson 2000, Hawkes et al. 2005, Shah et al. 2009). This frequency-dependent invasion resistance is often called a positive feedback (Eppstein and Molofsky 2007). The order of species arrival can greatly affect these feedbacks by initiating priority effects, resulting in a landscape that may be composed of a mosaic of sharply-edged areas dominated by different species each able to resist colonization by other species (Chase 2003). In my work I observed that an exotic at high abundance can reduce the fitness of a native relative to its conspecifics, promoting its dominance (Chapter 3).

Importance of exogenous drivers. Disturbances both natural and novel play an important role in shaping communities and ecosystems (Figure 1 "Exogenous Drivers"; Sousa 1984). Disturbances can influence community dynamics by altering the environmental filters that structure a community and by acting as an additional filter on species and species traits within a community (Diaz et al 1999; White & Jentsch 2004). Sequential disturbances acting upon a system can interact to produce synergies that can alter a community's response and resilience to a disturbance (Paine et al. 1998, Davies et al. 2009). Identifying when these interactions will occur and understanding the potential synergistic effects is critical for land management under continuing global change (Turner 2010). In my dissertation research, I specifically focused on a large fire that occurred after a severe drought (Chapter 4) and nitrogen deposition (Chapters 3 & 6).

Initial recovery after a disturbance commonly depends on the species present prior to a disturbance leaving residual individuals, either vegetatively or in the seed bank (Figure 1 "Indirect effects"; Noble and Slatyer 1980, Turner et al. 1998, Meiners et al. 2002). In cases where natives and exotics differ in life history, this balance of residual components (vegetative, seed bank) is thought to influence interactions between native and exotic species during the “invasion window” following a disturbance (Meiners 2007, Tognetti et al. 2010) and to result in a classic competition-colonization tradeoff (Levins and Culver 1971). I observed that the propagule pressure of neighboring exotic dominated patches thwarted the recovery of natives after an extreme disturbance (Chapter 4).

Exogenous factors, which occur at large spatial scales, can also interact with finer scale processes, to create cross-scale interactions, further complicating our ability to predict responses to disturbances or stress events (Peters et al. 2007). These events can facilitate invader establishment if these events alter the local scale mechanisms that maintain a community’s dominance (Diez et al. 2012). For example, atmospheric N deposition can increase ecosystem N availability and increase ecosystem productivity, resulting in a more competitive environment that favors taller, faster growing and often exotic species (Goldberg and Miller 1990, Suding et al. 2005). Soil microbial communities are also sensitive to environmental change (Vasquez et al. 2008) and changes in these communities either via altered soil resource availability as with N deposition or altered plant-plant interactions within the host community can facilitate the establishment of exotic species (Siguenza et al. 2006). Within my work, I observed that increased N availability altered competitive interactions between native and exotic species to not only facilitate the establishment of the exotic within native populations but to maintain exotic dominance (Chapter 3). I also observed that soil communities from high N sites reduced the positive effect that native home soils had on native growth potentially facilitating the establishment of an invader at high N (Chapter 5).

Research Context. Within my dissertation I explore how local-scale processes can interact with exogenous drivers to ultimately influence plant invasions and management within a California grassland (Figure 1). This work was motivated by a desire to understand what mechanisms contribute to the patch dynamics that I observed within a grassland along Loma Ridge within the Irvine Ranch Land Reserve in Orange County, California (N:33.7501, W:-117.71787, Figure 2). This grassland contained multiple areas dominated by either exotic (*Avena fatua* L. & *Bromus diandrus* Roth) or native (predominantly *Stipa pulchra* Hitchc.) grasses in close proximity to one another (nomenclature follows Baldwin et al. 2012). Traditionally, local scale interactions have been used to explain the establishment success of invaders as well as the invasion resistance of a site. However, in light of environmental change, this approach has been expanded to recognize that invaders can be passengers of change, where exogenous drivers can facilitate the spread of invaders (MacDougall and Turkington 2005, HilleRisLambers et al. 2010). Additionally, synergistic interactions between exogenous drivers and invader impacts may shift processes thwarting the recovery of natives, resulting in regime shifts (Diez et al. 2009). Below I will provide an overview of both the local and regional processes that I addressed to create a more holistic process based assessment of site invasion and restoration.

In Chapter 2, I provide a framework for how to identify and incorporate recovery constraints into restoration efforts. Invasive species management programs are widely incorporated into management plans; however, the success of these programs hinges on the ability to identify when a system will be able to recover after invader control and eradication efforts and when further intervention will be necessary to aide recovery. Invasive alien plants can alter ecosystem attributes to produce strong legacy effects that prevent the recovery of a system. Identifying recovery constraints can help improve how ecological theory - assembly rules, ecological succession, and threshold dynamics – can be used to guide restoration efforts.

In Chapter 3, I investigate how species effects on resources can interact with increasing nitrogen (N) availability to influence either invasion resistance, coexistence or invasion dynamics. Using an experimental approach where I manipulated both species dominance (either native *Stipa pulchra* or exotic *Avena fatua*) and resources (soil N and light availability), I was able to examine whether N enrichment would facilitate the invasion of the exotic via interactions with species' effects on resources. In Chapter 4, I investigate how exotic annuals are able to capitalize on the invasion window after a disturbance, by combining measurements of species composition and propagule pressure.

In Chapter 5, I examine with a greenhouse feedback experiment how soil resources and plant-plant interactions may alter plant-soil feedbacks for the native, *Stipa pulchra*, and exotic, *Avena fatua.* In Chapter 6, I conduct a field experiment to explore whether competitive interactions or soil resource availability are constraints for the recovery of native species after a large-scale disturbance.

Implications for Invasion and Management. My goal for this dissertation was to provide a tool to understand not only why native resident communities are invaded but also how to reduce the resistance of invaded communities and increase the resistance of native communities. Within my work, I found that increased N availability will likely facilitate exotic invasion as 1) it dampens the impact that the resident native has on soil resources, 2) it alters the competitive interactions between the resident native and exotic invader, and 3) it minimizes the positive effects of the native-conditioned soil community on native growth. Additionally, I observed that increased N can increase exotic fitness three-fold. Through small-scale field experiments, I found that management efforts should target multiple recovery constraints to enhance the establishment of natives within invaded areas. Seed additions and soil N reductions were able to increase the establishment and fitness of some natives, but may not be sufficient to promote full native recovery. Future efforts should also include plans to mitigate the negative effect that exotic conditioned soil has on native plant growth. By taking a more holistic approach I was able to tease apart within my system how multiple fine scale processes may interact with broad scale environmental changes to determine when we would see invasion, coexistence versus invasion resistance to guide future management efforts.

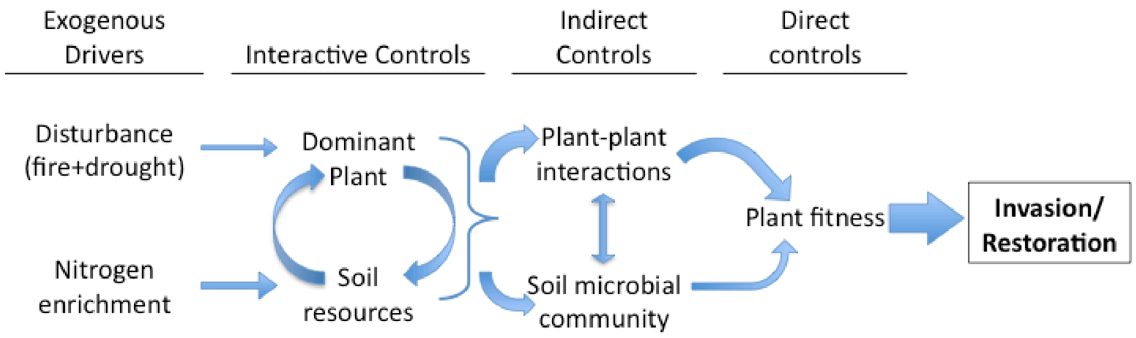


Figure 1. The major factors controlling plant invasions and potential restoration efforts addressed within my dissertation. These controls span multiple factors, ranging from local to regional spatial scales, which influence plant fitness and ultimately whether invasion will take place. Thickness of the errors indicates the strength of effects that I observed throughout my dissertation.

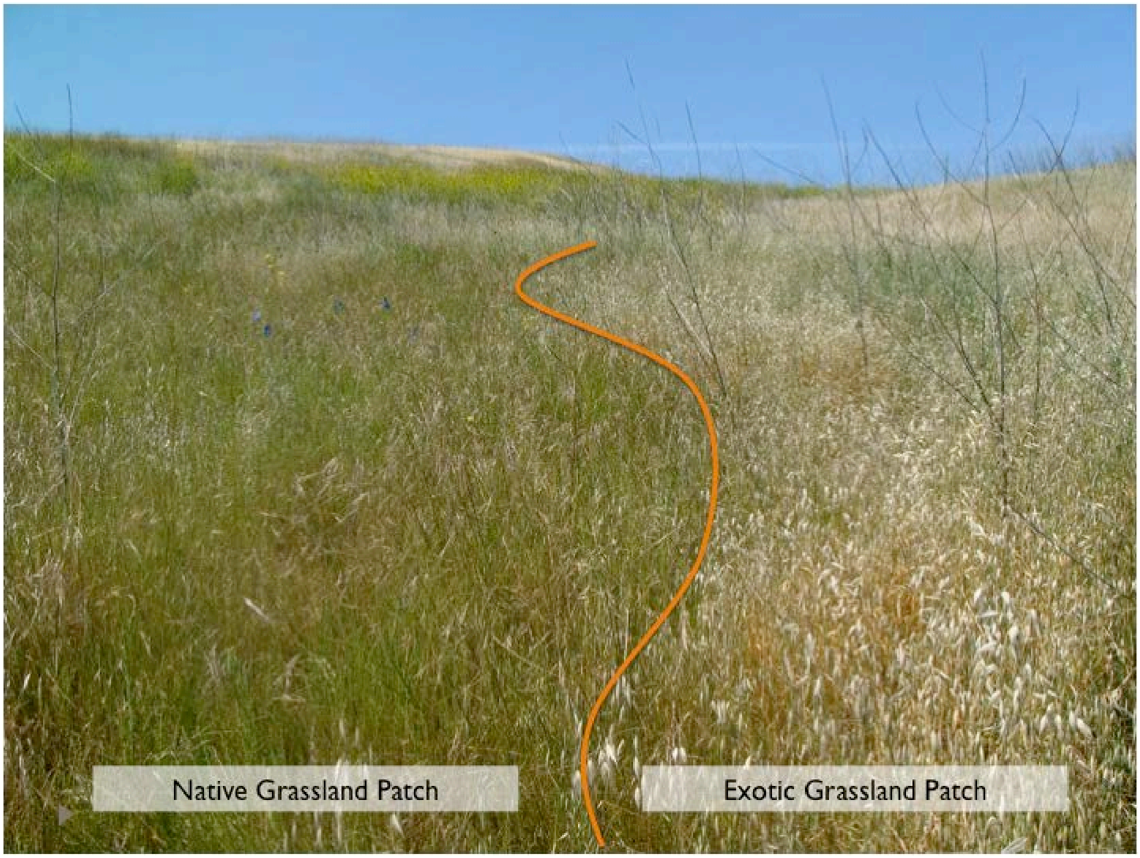


Figure 2. Example image of the mosaic pattern of native and exotic dominated grass patches along Loma Ridge in Irvine, CA. The native patch is dominated by *Stipa pulchra*, while the exotic patch is dominated by *Avena fatua*. This image was taken near the intersection of Loma Ridge Jeep Trail & Shoe String Rd in the Irvine Ranch Natural Landmark (N: 33.7525, W: -117.72372).

Chapter 2

Restoration within Protected Areas: When and How to Intervene to Manage Plant Invasions?

Introduction

Protected areas serve as the primary method to maintain and protect global biodiversity (UNEP-SCBD 2001). Therefore, an important goal in protected areas is to minimize threats to biodiversity and maintain ecological communities in their natural states (Lockwood et al. 2006). Protected areas can manage certain threats such as deforestation or poaching, but even the most well-managed reserves are still susceptible to threats such as climate change, pollution, and invasive alien species that do not recognize these conservation boundaries and fencelines. I focus on managing one of these threats, invasive alien plant species, in protected areas. In response to this threat, many protected areas have implemented large-scale invasive species management programs that employ prevention, eradication, and control strategies aimed at slowing or stopping the process of invasion (Foxcroft and Richardson 2003, Doren et al. 2009b).

Increasingly, a challenge in this process is that simply removing the invasive species is not sufficient to restore native biodiversity. A recent review by Kettenring and Adams (2011) found that invasive removal successfully reduced the cover of invasive alien plants (IAP), but did not always result in native species recovery. Further intervention – with a focus on restoration – may be necessary to take into account the impacts an invader has on a system (D'Antonio and Meyerson 2002), as well as address recovery constraints of the native community. However, these additional intervention actions can be costly in terms of time and money and, in some cases, they have unintended consequences and actually slow recovery (Zavaleta et al. 2001, Hobbs and Richardson 2011). Integrating additional intervention efforts within an existing protected area management plan can be complicated by a variety of factors such as limited resources (e.g., staff, infrastructure), legal mandates under IUCN management categories, or differing agendas among the stakeholders in the governance group (Keenleyside et al. 2012). The isolated nature of protected areas requires intervention efforts to be a concerted endeavor with agencies/land owners outside of the reserve, further complicating the success of management efforts.

In this chapter, I focus on this conundrum: when should we expect a system to recover without additional restoration efforts after invasive species control efforts? And when is further intervention necessary for recovery? Resources are often scarce for protected areas, with eradication and control of invasive species often consuming a disproportionate amount of reserve budgets (D'Antonio and Meyerson 2002). Identifying necessary points of intervention prior to action is therefore critical for successful protected area management. We begin by providing an overview of invader impacts that may constrain and preclude the recovery of a system after IAP management. I then explore key ecological theories that can be used to guide restoration strategies. Finally, I discuss how land manager s could adjust restoration efforts depending on the constraints present in the system.

In this chapter, I consider restoration to include both IAP control and eradication efforts as well as additional actions to aid native recovery. As emphasized elsewhere in this volume, invader management plans in protected areas often include control and eradication efforts in tandem with native recovery efforts. Here, I focus on restoration after the invaders are removed or reduced. The key questions are thus: when will passive recovery following these efforts be sufficient to recover desired native communities, and when will active intervention (*sensu* Suding 2011) be needed?

Invader Impacts and Recovery Constraints. As protected areas operate under the mandate to protect local biodiversity, the continuing and growing threat of IAP invaders on native biodiversity has made IAP management a priority for protected areas (Macdonald et al. 1988, Vitousek et al. 1997b, McNeely 2001). Understanding invader impacts on ecological communities is an important first step in understanding how native communities may recover following IAP control. I particularly focus on IAP legacy effects in protected areas, where the impacts of invasion persist even after invader control or eradication. In these cases, removing the invader may not always lead to successful recovery of the degraded system (D'Antonio and Meyerson 2002); additional management and restoration actions may be necessary to put the native community on a path to recovery (Suding et al. 2004). Alternatively, if an IAP does not have strong legacy effects, additional efforts may not be necessary and native communities should be expected to passively recover following control efforts. Importantly, the impacts of invasion may occur either progressively with invader abundance or abruptly once the invader reaches a certain abundance threshold (D'Antonio and Chambers 2006, Didham et al. 2007). Consequently, whether active or passive restoration is necessary may depend on the pattern as well as the nature of legacy effects.

Native species recovery may often be limited by dispersal following IAP control (Galatowitsch and Richardson 2005, Traveset and Richardson 2006). Source populations of native species may be far from the restoration area (McKinney and Lockwood 1999) or seed dispersal networks may be altered in the invaded area (Traveset and Richardson 2006, McConkey et al. 2012). For example, in Australia, recovery of coastal dune communities invaded by the South African bitou bush (*Chrysanthemoides monilifera* subsp. *rotundata*) is limited by poor seed dispersal from existing native vegetation (French et al. 2011), and in New Zealand, native shrublands dominated by kanuka (*Kunzea ericoides*) have a different composition and a smaller abundance of the avian seed dispersers compared to the gorse (*Ulex europaeus*) invaded stands (Williams and Karl 2002). Additionally, native seed bank at a restoration site could be diminished if natives have been absent or in low abundance, reducing the potential for recovery from *in situ* germination (D'Antonio and Meyerson 2002). In southern California, passive recovery of the native coastal sage scrub community is limited due to the depauperate native seedbank in long term invaded exotic grassland sites (Cione et al. 2002, Cox and Allen 2008).

Plant invaders can alter disturbance regimes, which may create positive feedbacks that promote invader success (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). These feedbacks must be disrupted to allow the recovery of a system (Suding et al. 2004). A widespread example occurs when annual grass invaders increase the intensity and frequency of fire (D'Antonio and Vitousek 1992). In the Western United States, for example, exotic annual grasses increase fuel loads, which promotes a fire frequency for which the resident community is not adapted (Whisenant 1990). Conversely, IAPs can also impact disturbance regimes by suppressing disturbances (Mack and D'Antonio 1998). Pepper tree (*Schinus terebinthifolius*) invasion in Florida's Everglades National Park has suppressed fire intensity by decreasing fuel loads (i.e., understory vegetation), which enhances its own recruitment (Doren and Whiteaker 1990). In these cases, the disturbance regime may not recover following IAP control, and additional actions may be needed to re-establish the disturbance regime needed to support the native community (Davies et al. 2009).

IAPs can also impact the physical structure of soils by increasing erosion rates or sedimentation rates and directly affecting substrate stability (D'Antonio et al. 1999), resulting in soil legacies (*sensu* Corbin and D'Antonio 2004c). For example, while increased sedimentation can promote succession and facilitate the establishment of native species in degraded forests in Algiers (Wojterski 1990), increased erosion rates can limit recovery by eliminating habitat for native species and promoting the establishment of introduced species in the South African fynbos (Macdonald and Richardson 1986).

Soil legacies can also influence belowground biological processes that promote IAP abundance and stall native species recovery (van der Putten et al. 2007, Inderjit and van der Putten 2010). An invader can be successful because it is able to escape soil pathogens (Klironomos 2002), and it may also alter pathogen incidence in the native community to reduce competitive effects and facilitate its spread (Eppinga et al. 2006, Mangla et al. 2008). Pathogen loads may slow the recovery rates of communities, as they continue to influence the performance of native species even after IAP removal (Malmstrom et al. 2005). IAPs can facilitate their invasion by allelopathy (i.e., the release of phytotoxins, which inhibit the growth of neighboring plants; Callaway and Ridenour 2004). For example, high impact invader spotted knapweed (*Centaurea maculosa)* releases a compound that inhibits root growth of its neighboring plants (Bais et al. 2003). Additionally, garlic mustard (*Alliaria petiolata),* a widespread invader in North American forests, secretes compounds that inhibit the symbiotic mycorrhizal associations of native plants. These altered relationships can prevent the recovery of the community once the invader has been removed due to residual toxins (Perry et al. 2005). Other invaders can alter soil properties such as salt concentrations or soil pH, reducing the potential for subsequent colonization by native species (Vivrette and Muller 1977, Conser and Connor 2009).

Soil legacies also include invader impacts on biogeochemical cycles that alter resource availability (Mack et al. 2001, Ehrenfeld 2003). Nitrogen cycling rates are regularly increased by invaders by altering the microbial community (Hawkes et al. 2005), altering litter quality (Sperry et al. 2006), or directly by nitrogen-fixing species (Vitousek and Walker 1989, Le Maitre et al. 2011). Increased nitrogen availability can result in positive feedbacks that maintain the invaded state, thwarting recovery efforts (Clark et al. 2005). For example, in temperate grasslands in Australia, exotic annual species that invade native perennial tussock grasslands can alter nitrogen cycling to favor their own growth. These nutrient changes are sufficient to push the system past a threshold, preventing the recovery of native grasses (Prober et al. 2009). Lastly, invaders can also alter the hydrology of a system via altered transpiration rates, rooting depths, phenology, and growth rates (Levine et al. 2003). Salt cedar (*Tamarix* spp.) invasion in the southwestern United States has resulted in higher transpiration rates and marginal water loss due to the salt cedar's deeper root system in this water limited system (Zavaleta 2000).

Ecosystem Models in Restoration. While it is clear that many IAPs have strong legacy effects that can influence the recovery of native communities, it is also important to put these effects in the context of ecological processes that guide the path to recovery (Young et al. 2005, Hobbs et al. 2007, Suding and Hobbs 2009). Conceptual models of ecosystem dynamics such as assembly theory, ecological succession, and threshold dynamics can guide restoration projects by providing insights into these ecological processes (Figure 1). In the following paragraphs I explore these three concepts and how they can guide decisions about when and how to intervene in protected areas following invasive plant control efforts. For each, I first present the basic framework, then a case study examining application to restoration in protected areas.

Assembly Rules

Assembly theory focuses on how a suite of processes (e.g., dispersal, disturbance, environment, competition) influence, which species are able to establish over time (Young et al. 2001, Temperton et al. 2004, White and Jentsch 2004, Hobbs et al. 2007). This framework integrates these processes into a series of filters (dispersal, environmental, and biotic) that act at varying spatial scales, which can explain which species from a regional species pool (large scale) are found in the local community (small scale, Weiher and Keddy 1995, Diaz et al. 1998, 1999). In the context of native species recovery following IAP control, recovery requires that filters at each scale allow native species to establish and persist (Figure 1b). Additional intervention efforts would be focused on the filters that excluded the desired species from recovering (Figure 1b, dashed arrow).

Three general types of filters are emphasized in assembly theory. The first filter that species must overcome is dispersal: species must have dispersal traits that allow them to arrive at a site (Levine and Murrell 2003). As discussed above, invasive plants can increase the dispersal limitation of native species in many ways, creating new barriers to the dispersal filter for some native species. If a species is able to colonize a site, the next filter acting upon it is the environmental filter. To successfully cross the environmental filter, a species must have the suite of traits that allow it to survive the given environmental conditions (Weiher and Keddy 1995, Diaz et al. 1998, 1999). Soil legacies of invasive plants, such as erosion and resource cycling impacts, can alter this filter. An extension to the environmental filter is the disturbance filter (White and Jentsch 2004), which invasive species may similarly alter. The final filter in assembly theory is the biotic filter, which restricts the community to those species that can coexist in the presence of interspecific interactions (MacArthur and Levins 1967, Tilman 1990, Chesson 2000). Under the biotic filter, competitive interactions would limit the co-occurrence of functionally equivalent species due to niche limitation resulting in limited similarity among species within community (MacArthur and Levins 1967). Under situations where invasive species have been controlled or eradicated in protected areas, we would expect that this biotic filter would be less of a consideration compared to the other filters, but it would be important to manage were reinvasion possible.

The efficacy of active intervention efforts in restoration (e.g., species palette for planting, selection of planned disturbance to limit competitive interactions) can be assessed in this assembly filter framework by equating restoration actions with changes in assembly filters (Funk et al. 2008). For example, seed addition or planting of native species can be viewed as changing the dispersal filter at a site. Similarly, a trait-based approach could increase the success of restoration efforts areas where managers fear invasive species could re-invade following control efforts by identifying a suite of native species with traits similar to the IAP to enhance the invasion resistance of the community, thereby strengthening the biotic filter (Funk et al. 2008).

Case study 1: California Grasslands

Protected areas such as county parks and reserves within California are often imbedded within a highly fragmented landscape (Greer 2005). In California protected areas, alien annual grasses have the potential to gain access to the interior of natural areas by initially colonizing disturbed roadside areas (Gelbard and Belnap 2003). Roadsides can have large inputs of atmospheric nitrogen deposition (Pearson et al. 2000), which can interact with local grassland's N cycling to increase N availability (Sirulnik et al. 2007), and further promote these annual grasses (Padgett and Allen 1999). Furthermore, prolonged dominance of alien grasses within a site can reduce the seedbank of native species and prevent the recovery of a system once the grasses have been removed (Cione et al. 2002).

To evaluate if the biotic filter can be manipulated to slow or stop the re-invasion of exotics after control, Cleland et al. (2012) conducted a restoration experiment along a roadside edge of the Laguna Coast Wilderness Park in southern California where they manipulated nitrogen availability and added native seeds representing different functional groups (annual/perennial grasses, early/late forbs and N-fixing legumes). In the first year, they removed alien annual grasses and forbs. Then in the second year, they allowed alien species to colonize naturally. Native communities with low N availability and in which early forb seed was added best resisted re-invasion. Thus, they found that by altering resource availability and adding species that have similar phenology to the problematic invader they could manipulate the biotic filter to increase invasion resistance.

Ecological Succession

Successional dynamics, the changes in species composition within a community over time, have been a classic and focal question in ecology since the 1900s, (Cowles 1899, Clements 1916, Gleason 1926). Succession traditionally describes the patterns of compositional change after a disturbance (Clements 1916, Pickett et al. 1989) but recent studies have gone beyond describing the patterns to identify the mechanisms, which influence these patterns (Connell and Slatyer 1977, Tilman 1988, Pickett et al. 2009). As successional theory has expanded to incorporate the possibility of multiple successional pathways versus a single climax community (Glenn-Lewin et al. 1992), comparing and analyzing successional trajectories has been adopted to describe the temporal change in community composition (Hobbs and Mooney 1995). Once a disturbance occurs at a site, the availability of safe sites and propagules for colonization in conjunction with the impacts of established species determine subsequent successional dynamics (Pickett et al. 1987). In the context of whether to intervene following invasive species control, additional intervention activities can be viewed as either altering or initiating any of these recovery processes (del Moral et al. 2007; Figure 1a).

Ecological restoration can take a variety of approaches to manage succession toward a desired target. The first and simplest approach is to allow succession to occur unaided (spontaneous succession, Prach et al. 2001) and should be a viable option if most abiotic and biotic functioning remain intact after invasive species control (Lockwood and

Samuels 2004, Prach and Hobbs 2008). However, in the case of large-scale invasions, natural succession is unlikely to be a viable option as legacies from the invader may influence recovery (Zavaleta et al. 2001). When legacies are present another approach is to assist succession via manipulations to the physical environment and to biotic processes that may be important within the target system (technical reclamation, Prach et al. 2007). Technical reclamation may be necessary if invasion has resulted in the complete loss of any of the overarching processes governing succession (e.g., availability of safe sites, propagules, and species impacts; del Moral et al. 2007, Prach and Hobbs 2008). The third approach, assisted succession, is a combination of technical reclamation and spontaneous succession in which site conditions are initially modified to support native species but subsequent succession is allowed to occur naturally (Prach et al. 2007; Figure 1a dashed line). This approach has been implemented within rangeland invasive plant management, by pairing removal efforts with post-removal restoration activities (Sheley et al. 2010). While this framework is similar to assembly theory in that it emphasizes identification of processes that constrain recovery, it also emphasizes trajectories of community development over time.

Case Study 2: South African Fynbos

The fynbos vegetation in the Cape Floristic Region of South Africa is highly impacted by exotic trees and shrubs (Acacia spp; Macdonald 1984, Le Maitre et al. 2011). Acacias are nitrogen (N)-fixing plants, which can increase soil fertility after an extended presence in an area (Yelenik et al. 2004). They also have a large impact on water resources, as they consume more water than the native vegetation (Le Maitre et al. 2000). Under the national "Working for Water" program, *Acacia* spp. and other woody invasive plants have been targeted for removal (Turpie et al. 2008). Clearing of these invaders is often a combined effort of cutting down the tree/shrub and, for those species that resprout, applying herbicide to the stumps with the felled biomass left on site. It can also involve the removal of the felled material and/or burning (Macdonald 2004). Cleared sites are often allowed to recover spontaneously after treatment; however, the success of passive recovery is often dependent on the type of treatment (i.e., spontaneous succession was the most successful with clearing and removal and the least successful under burning (Blanchard and Holmes 2008). Blanchard and Holmes (2008) found that once the biomass was removed, native species had space to establish and assisted succession approaches were needed. For example, seeding after burn treatments to overcome dispersal constraints can increase the presence of native fynbos vegetation and enhance natural recovery; however, continuous eradication efforts are needed until the large *Acacia* seedbank is reduced as natural wildfires may continue to promote the establishment of *Acacia* after initial removal (Milton and Hall 1981).

Threshold Dynamics

Ecological thresholds are a breakpoint between two systems that, when crossed, result in an abrupt change in community states (Holling 1973). Thresholds occur due to positive feedback mechanisms, which make systems resistant to change (Folke et al. 2004, Suding et al. 2004). While successional models and recovery pathways apply to many situations of recovery following IAP control, threshold models can help explain why some systems are not able to recover once the invader has been removed (Prober et al. 2009). In the context of these "stuck" systems, threshold models point to the importance of breaking these positive feedbacks in order to facilitate recovery (Figure 1c).

A useful framework for incorporating ecological thresholds into management has been to divide thresholds into two stages. The first stage is the biotic threshold, which can be identified by changes in vegetative structure or composition (Friedel 1991, Whisenant 1999). The second stage is an abiotic threshold, which identifies changes in ecosystem functioning (Whisenant 1999). Because impacts on functioning are thought to lag behind biotic changes, a system is thought to first encounter the biotic threshold and subsequently the abiotic (Whisenant 1999, Hobbs and Harris 2001, Briske et al. 2005). IAP's that trigger biotic threshold changes may be easier to control than those that cause biotic and abiotic threshold changes. Invaders that cause the system to cross both thresholds (ecosystem engineers, *sensu* Jones et al. 1994) make the success of restoration efforts highly uncertain (Ehrenfeld et al. 2005, Kulmatiski 2006, Doren et al. 2009a). Once management has identified key variables that can indicate whether a threshold has been crossed, this knowledge can be used as management thresholds to identify when and what management efforts are needed to increase the success of control and subsequent restoration efforts (Foxcroft and Richardson 2003, Doren et al. 2009b).

Case Study 3: Australian Subtropical Rainforests

One of the world's most notorious invaders, *Lantana camara,* has invaded and replaced much of the native vegetation in the subtropical forests in eastern Australia (Lowe et al. 2000, Bhagwat et al. 2012). *Lantana* was introduced as an ornamental shrub in the mid-19th century (Swarbick 1986) but has rapidly spread to the detriment of native diversity, including protected areas within Australia's national parks. Many of the national parks within eastern Australia are isolated within a highly disturbed system, a problem common to many protected areas globally (Fox et al. 1997). Edges between the reserves and disturbed areas (e.g., old agricultural fields in Australia) make reserves vulnerable to weedy invaders such as *Lantana*, which readily spread across disturbed landscapes (Gentle and Duggin 1997, Stock 2004).

However, this landscape also provides an opportunity to investigate the dynamics that allow this invader to invade pristine habitats. Stock (2004) and Gooden et al. (2009) monitored *Lantana* and native plant abundance in national parks in eastern Australia and were able to identify two separate thresholds. After measuring *Lantana* cover and canopy cover in gaps in two national parks, Stock (2004) identified an a first invasion threshold: forests whose canopy cover is 75% native species can prevent the establishment of *Lantana*, because the woody invader is shade intolerant in those forests. If *Lantana* reaches 75% cover, however, the system crosses a second biotic threshold identified by Gooden et al. (2009) in which native species richness falls dramatically, likely due to *Lantana* effects on soil fertility (Bhatt et al. 1994) and soil seed banks (Fensham et al. 1994). These thresholds, which identify when a community can resist invasion and when invader impacts begin to increase dramatically, are being used to guide an integrated management plan (Stock 2005).

Addressing Recovery Constraints in the Context of the Three Models. The ability of ecosystems to recover after IAP control greatly varies and is often contingent on the system's intrinsic rate of recovery, its level of degradation, and its surrounding matrix

(Jones and Schmitz 2009, Holl and Aide 2011, Gaertner et al. 2012). This variability makes it difficult to assess when land managers should intervene and implement additional restoration practices or leave a system to recover naturally (passive restoration, *sensu* Suding 2011). For example, in the southwestern United States, invader removal without any paired plantings of native flora can detrimentally affect local fauna (Zavaleta et al. 2001), and yet, active plantings in the tropics may prevent the establishment of native flora and slow natural recovery (Murcia 1997). Furthermore, within protected areas, additional complicating factors such as land use and pollution are either well documented or less severe than in non-protected areas. Therefore, restoration efforts conducted within protected areas after IAP removal can help improve our collective understanding of invader impacts and recovery constraints. In this section, I suggest a series of steps to decide when additional intervention following IAP control may be needed.

First, an understanding of the extent of IAP impacts and whether they will persist following invader removal is critical (Sheley et al. 2010). A holistic assessment should try to identify the causes of the invasion as well as impacts of the invasion (see invader impacts section above; James et al. 2010). If a holistic assessment was not initially available, small-scale experiments can be used to identify restraints (Kettenring and Adams 2011). Simply observing the natural recovery of a system after control efforts would also aide the decision of whether or not to intervene when assessments are not available (Holl and Aide 2011). If monitoring indicates natural recovery, land managers can use successional theory to make inferences about the trajectory of the system (Sheley et al. 2006, Prach and Walker 2011). However, if monitoring identifies invader legacies, the success of management efforts is contingent on effectively prioritizing and addressing those recovery constraints (Figure 2a; Suding et al. 2004).

Identification of constraints can be done through knowledge of natural history, experimentation (Gaertner et al. 2011, Kettenring and Adams 2011) or research from other sites (e.g. recent reviews of the effects of the invaders *Acacia* (Le Maitre et al. 2011) and *Lantana* (Bhagwat et al. 2012) on ecosystems). If one single factor seems to strongly constrain recovery, natural recovery should be fairly straightforward if land managers can address the single constraint (Prach et al. 2001, Lockwood and Samuels 2004). Successional theory and assembly theory would be helpful in guiding restoration efforts with single constraints (Suding and Hobbs 2009). However, if multiple constraints are present, it is important to assess whether these constraints can be addressed independently or need to be addressed in tandem (Suding et al. 2004). If multiple constraints synergistically thwart the recovery of a system, it would be essential to address the constraints in tandem to disrupt any feedbacks that are preventing recovery (Figure 2a; Suding et al. 2004).

Constraints can operate at multiple spatial and temporal scales (Suding and Hobbs 2009), and processes operating at one spatial or temporal scale can interact with processes operating at another scale to create strong internal feedbacks that prevent the recovery of the system (cross-scale interactions; Peters et al. 2007). In a hypothetical example, if an invader disrupted dispersal processes and produced soil legacies via allelopathy, successful restoration efforts would have to address both the soil condition as well as the dispersal constraint. Threshold models address strong internal feedbacks and nonlinear dynamics within ecosystems and would be helpful in guiding restoration efforts with interacting constraints (Suding and Hobbs 2009). If the constraints do not interact, it would be important to prioritize constraints, and assembly theory could help elucidate which constraints and potential restoration approaches could be addressed based on how the degraded system has deviated from the historical environmental and biotic conditions (Lockwood and Samuels 2004). However, projects that incorporate several restoration actions are often more successful; therefore if resources are available, it would be wise to tackle multiple constraints (augmentative restoration; Bard et al. 2004, Buisson et al. 2008). While these approaches can help a land manager make better *a priori* decisions about what restoration activities to undertake, this approach is not foolproof and should always incorporate monitoring and re-assessment to ensure that the system is moving in the desired direction.

Case Study 4: Sustainable control efforts of Artichoke Thistle (Cynara cardunculus) in Orange County, California

Artichoke Thistle was introduced into southern California in the nineteenth century and has become a problematic invader across local grasslands (Thomsen et al. 1986). It is a perennial species with a deep taproot (~1.5m) and large inflorescences (up to 50 per rosette; Marushia and Holt 2006) filled with up to 800 wind dispersed seeds (Kelly 2000). It forms dense species-poor stands (Bowler 2008). Within the Nature Reserve of Orange County, it has invaded over 4000 of the 37000 acres of protected open space and its control has dominated the Reserve's budget for invasive species management (McAfee 2008). The primary control method since 1994 has been direct herbicide application with the assumption that native communities would passively recover. However, after 13 years native species did not recover in all treated areas; instead, the abundance of other alien plants increased (Seastedt et al. 2008). In an effort to implement more effective management activities for native grassland recovery, potential constraints were further identified using other published research studies. For example, seed limitation is often a constraint for native grass populations across California (Seabloom et al. 2003a, Seabloom 2011). Additionally, Potts et al. (2008) identified that litter quantity and quality changes due to artichoke thistle invasion, which can negatively impact native recovery (Bartolome and Gemmill 1981, Coleman and Levine 2007). These findings can be integrated into a potential management plan for efficient and sustainable management of treated areas (Figure 2b), where the passive recovery approach would be replaced with one where seed limitation and soil legacies constraints are both prioritized within the reserve.

Conclusions. Ecosystems globally are undergoing rapid changes due to global change drivers (i.e. CO_2 enrichment, atmospheric nitrogen deposition, climate changes, land use, and biotic invasions; (Sala et al. 2000). Among these drivers are invasive species, which are an increasing threat to natural and working landscapes as the globalization of trade and interactions with other global change drivers increases the opportunities for introductions (Levine and D'Antonio 2003, McNeely 2006). A small fraction of those invaders have the potential to trigger large changes in ecosystem functioning as they spread across a landscape (Williamson 1996) and can contribute to the degradation of native communities (McNeely 2001). Protected areas have the unprecedented burden of minimizing these negative invader impacts as they are tasked with the goal of protecting and maintaining the globe's biodiversity.

Here, I emphasized ways to determine whether additional intervention is needed for native recovery following IAP control in protected areas. Multiple lines of evidence need to be weighed to best gauge when and where to invest in additional intervention approaches and when to stand back and allow the native system to recover naturally. This decision-making is not clear- cut but can be based on several ecological frameworks describing how communities are assembled and recover over time. Protected areas benefit from a holistic management approach, which addresses IAP detection, sources of invaders, potential external stressors, and management thresholds dictating when management efforts need to be initiated (Zavaleta et al. 2001, Foxcroft and Richardson 2003, Clewell and McDonald 2009). Worldwide efforts to evaluate the effectiveness of management within protected areas (Hocking et al. 2000) provide a unique opportunity to assess the link between ecological theory that frame the process of recovery and restoration actions.

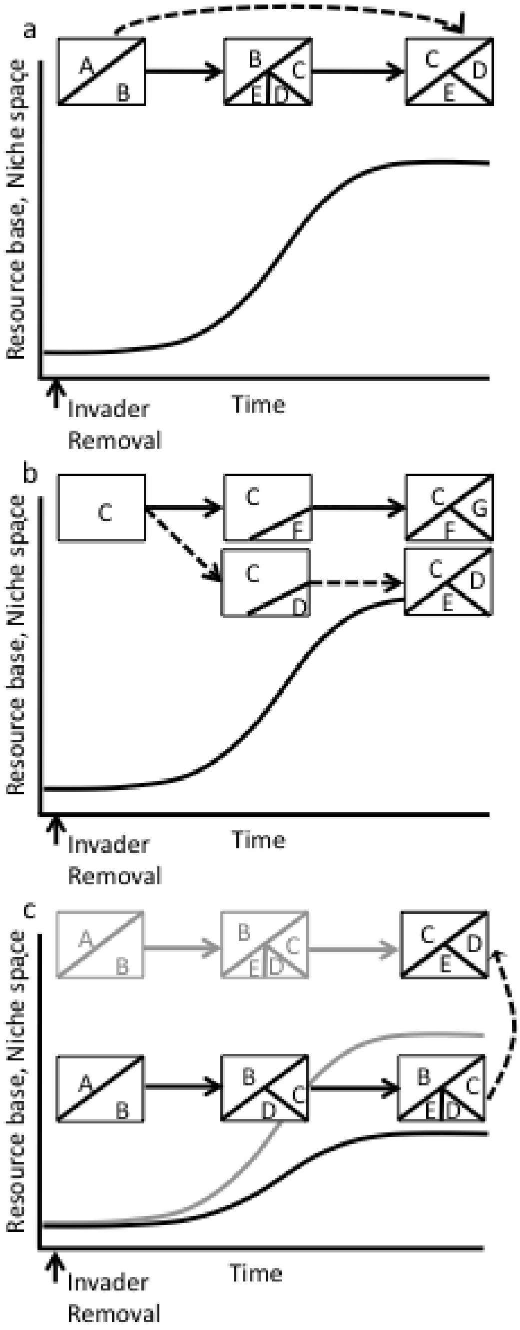


Figure 1. Recovery trajectories after invader removal, assuming little invader impact (a) or a legacy of invader impacts (b,c). Species composition is symbolized by the capital letters and abundance by proportion of each square; the desired goal community is C/E/D. Solid lines indicate scenarios with passive restoration after IAP removal; dotted arrows indicate restoration intervention. We present scenarios consistent with each of the three ecosystem models of recovery. Successional theory (a) is most appropriate in systems where there is little expectation of strong invader impacts. In (a), successional theory assumes directional

change in species composition over time. If the natural recovery takes too long, land managers can intervene to accelerate recovery (dashed arrow in a). In systems impacted by invader legacy affects (b,c), assembly theory and threshold theory may be most appropriate to guide restoration efforts. In (b), IAP legacies affect the order of species arrival. Active intervention can focus on adding species, affecting the order of species arrival, to guide the assembly process to arrive at the target community. In (c), recovery may result in a new undesired state due to invader legacy impacts, preventing the successional process that would occur naturally (gray boxes). A threshold model may be the most appropriate to apply in cases such as these, where multiple restoration activities would need to be done to overcome this feedback (dashed arrow, c). Modified from White and Jentsch 2004.

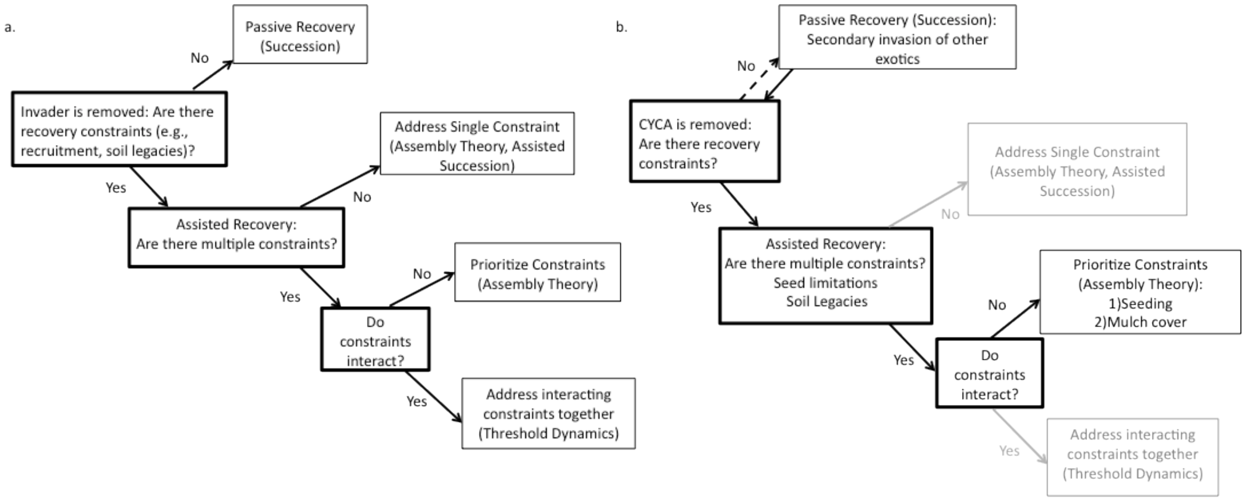


Figure 2. Decision Tree Model for assessing restoration activities following invader control efforts. Decision making nodes represent the assessment of identity, number of and interactions between recovery constraints (bolded boxes). At low and medium IAP abundances, control/removal efforts may be sufficient to return a community to its restored state (node 1: No intervention). However, at medium and high invader abundances management actions may not be sufficient to achieve the full recovery of the degraded system due to recovery constraints. A recovery constraint assessment can guide decisions for subsequent restoration actions (nodes 2 & 3). Ecological principles (listed in parentheses) can help inform which restoration tools to use. Decision Tree model for the control and restoration efforts for artichoke thistle (panel b). Initially management efforts relied on passive recovery (dashed line); however after observing the ineffective recovery of native species, the land managers decided to implement efforts to overcome constraints. Evaluation of constraints (supporting citations listed in case study) indicated two potential constraints, and after determining that they likely do not interact to synergistically thwart recovery, constraints were prioritized. Grayed boxes indicate paths that were not followed in this scenario.

Chapter 3

Invasion and dominance of an exotic annual, *Avena fatua*, into a native perennial *Stipa pulchra* stand under nitrogen enrichment

Introduction

Global environmental changes – rising temperatures, changed precipitation patterns, increased atmospheric deposition – are affecting ecosystems at an unprecedented scale and pace (Luque et al. 2013). A critical challenge is to understand and predict how these global changes affect the interactions among species that mediate ecological diversity (Suding et al. 2008, Tylianakis et al. 2008). Only recently applied to global environmental change (Adler et al. 2012), species coexistence theory provides a framework for understanding how changed environmental conditions may affect interactions among species. In the theory, the balance between niche differences (frequency-dependent stabilizing processes) and relative fitness differences (equalizing processes) governs species coexistence dynamics (Chesson 2000, Adler et al. 2007, Eppstein and Molofsky 2007). Because environmental conditions can affect the nature and extent of both fitness and niche differences through altered resource availability (HilleRisLambers et al. 2012), global environmental change should influence species interactions in a manner predictable by coexistence theory (Adler et al. 2012).

A less explored link between coexistence theory and environmental change is that a species can also influence its niche by altering its local environment (Chase and Leibold 2003). For example, species can reduce resource availability, alter rates of nutrient cycling, or influence the soil microbial community (Wedin and Tilman 1990, Hawkes et al. 2005, Chapman 2006). Species effects can either counteract or accelerate effects of global environmental change by either strengthening negative frequency dependence (negative feedbacks) or creating situations of positive frequency dependence (positive feedbacks), respectively (Ives 1995, Adler and Drake 2008). As these feedbacks can shift community structure, it is important to understand how and when environmental change can spur feedback effects.

Here, I apply coexistence theory to species invasions in the face of global change (Didham et al. 2005, MacDougall and Turkington 2005, MacDougall et al. 2009). I focus on increased nitrogen (N) availability, which is affecting large areas worldwide due to atmospheric N deposition (Bradford et al. 2012), and is often thought to increase the invasion of exotic species (Huenneke et al. 1990, Brooks 2003). I combined the "invasibility" criterion of coexistence theory (i.e. can species increase when rare; Siepieliski and McPeek 2010) with measures of species resource effects (i.e., can species influence resources when abundant; Tilman 1982) in a field experiment that manipulated N and light availability across species monocultures. I ask whether increased N availability facilitates the dominance of a widespread annual exotic grass, *Avena fatua*, at the expense of native perennial, *Stipa pulchra*, in California grasslands. I hypothesize that 1) species will coexist under ambient resource conditions due to niche differences, 2) increased N will facilitate invasion by minimizing species resource effects that contribute to niche differences, and 3) increased N will enhance dominance of the exotic by intensifying the its resource effects.

Methods

Study System

I used two dominant species found within California grasslands: *Avena fatua* L., an exotic annual grass and *Stipa pulchra* Hitchc., a native perennial bunch grass (hereafter *Avena* and *Stipa*, respectively; nomenclature follows Baldwin et al. 2012). These species are an excellent model to explore species coexistence dynamics, how coexistence may depend on positive feedbacks, and how these processes change along resource gradients. Both can occur as dominants in California grasslands (Heady 1977, Seabloom 2011). Past studies in California grasslands suggest that competitive rankings between exotic annual and native perennial grasses often vary depending on initial conditions (Dyer and Rice 1999, Hamilton et al. 1999, Abraham et al. 2009), indicating that frequency-dependent fitness differences may play a role in dominance of both exotic and native grasslands. Other studies have found evidence for niche partitioning mechanisms promoting coexistence (Harpole and Suding 2007) and fitness differences (Seabloom et al. 2003b). However, few studies have simultaneously investigated fitness differences resulting in either invasion or invasion resistance, and how these may depend on positive feedbacks between these two dominants (but see Corbin and D'Antonio 2004b, Thomsen and D'Antonio 2007).

Main Experiment

I set up a two-way factorial experiment at the South Coast Research and Extension Center (Irvine, CA 33˚40' N, 117˚49’ W) where I established 5 replicate blocks of monocultures of two species *Avena* and *Stipa* and manipulated nitrogen (N) availability (low, ambient, high). Irvine, CA experiences a Mediterranean climate with the growing season restricted to the period of precipitation, which falls between November and June. Annual growing season precipitation during the course of the study (2009, 2010, 2011) was 214mm, 175mm, 449mm and average growing season temperature was 16.0°C, 15.1°C, and 14.2°C, respectively (California Irrigation Management Information Services, http://wwwcimis.water.ca.gov/cimis/welcome.jsp). *Avena* monocultures were established by seeding at a rate of 10g/m^2, and *Stipa* monocultures were established by planting both adult (Mockingbird Nurseries, Riverside, Ca) and seedling (UC Irvine greenhouse) plugs.

I decreased N availability by adding sugar at a rate of 421 g C/m^2/yr^1 and increased N availability by adding slow release calcium nitrate at a rate of 6g N/m^2/yr^1 (Florikan®, Sarasota, FL). These nutrients were added at three different times over the growing season immediately before a rain event. Within the above experiment, I manipulated light availability as a split-plot factor by setting up shade cloth 80cm tall around the west and south facing sides of the plots as well as laying two strips of shade cloth 20cm wide across the length of the plot, directly over the phytometers (described below). Light availability was increased using vegetation tie-backs (Dickson and Foster 2011) and south-facing mirrors (16cmx49.5cm, Zadro™, Huntington Beach, CA; Lepik et al. 2004). In total, the experiment consisted of 90 1m^2 plots (2 vegetation x 3 N levels x 3 Light levels X 5 blocks). To ensure that N was the limiting soil resource, I applied one treatment of triple superphosphate every growing season at a rate of 4.5g*m^{-2}. The experimental plots were established in 2009, but no measurements were taken until the second year to allow the monocultures and resource treatments to better establish.

Reciprocal Invasions

In 2010 I planted 60 seeds of *Stipa* and 40 seeds of *Avena* in all plots. Due to poor germination, I additionally transplanted *Stipa* seedlings to ensure that there were at least 8 "invading" individuals in every treatment. I refer to these seeded target individuals as phytometers, hereafter. At the peak of the 2010 growing season, all *Avena* phytometers were harvested to measure aboveground biomass and to count the number of spikelets per individual as an estimate of fitness. Mortality of *Stipa* phytometers was recorded at peak biomass in April 2010 and any surviving *Stipa* phytometers were left in the plots to assess summer survivorship the subsequent winter (January 2011). I used an allometric relationship to estimate aboveground biomass for the *Stipa* phytometers in April 2010. For each seedling I counted the number of total leaves, height, and the number of ramets and additionally harvested 33 naturally recruiting *Stipa* seedling within the experiment for which I made similar measurements. A separate allometric relationship was calculated for each N treatment, using stepwise regression (low N: r^2=0.80; ambient: r^2=0.72; high N: r^2=0.86, fits listed in Appendix 1).

Resource measurements

To estimate N availability over the 2010 growing season, I measured resin extractable N using ion-exchange resins. Two resin bags (lycra mesh with 10.5g of resin) were buried 10cm below the soil surface in every plot in January. In May, all resin bags were collected (for a total of 116 days), extracted with 2 mol/L KCl, and analyzed by a continuous flow analyzer (A&L Western Laboratories, Modesto, CA). I measured soil moisture of the top 20cm every month from January to April using time domain reflectrometry (FieldScout TDR 100, Spectrum Technologies, Inc; Plainfield, IL). Additionally I measured photosynthetically active radiation (PAR, AccuPAR LP-80, Decagon Devices, Inc; Pullman, WA) above and below the vegetation canopy in every plot from January to April. I estimated light availability as 1 minus the proportion of the difference between the above and below canopy measurements to the above canopy measurement. In 2010, within the *Avena* plots I measured aboveground biomass by harvesting all biomass within a 25cm x 25cm subplot and drying the samples at 60$^{\circ C}$ for 48hrs. To estimate aboveground biomass of the *Stipa* plots, I established an allometric relationship using 30 *Stipa* adults from a separate neighboring experiment that also consisted of *Stipa* monocultures. I measured basal circumference and the number of reproductive culms for all the *Stipa* adults within the interior of each plot as well as for the 30 individuals that were harvested. Due to the planting scheme of the adult *Stipa* plugs in the plots, there was exactly one adult in every 25cm x 25cm area within the interior of each plot. I fit a single relationship across the experiment, which estimated biomass based on the number of reproductive culms (r^2=0.76, fits listed in Appendix 1).

Analyses

Resource Availability

To verify any resource differences within the experimental manipulations, I used proc mixed within SAS (version 9.3). For resin available N that had a single measurement over the growing season we ran a three-way ANOVA, with community type and N treatments as main factors and Light treatment as a split-plot factor, and block as a random factor. For soil moisture and light availability, which were measured multiple times over the growing season, I ran a repeated measures ANOVA with community type, N and Light treatments, and time as fixed factors and block as a random factor. To adjust for the time series data, I used maximum likelihood estimations, adjusted degrees of freedom to account the split-plot design as per Quinn and Keough (2002). I tested for interactions within the fixed factors using post-hoc Tukey's pair-wise tests.

To assess how all the resources varied simultaneously, I ran a principal components analysis (PCA) with SAS (version 9.3). Due to the correlation of monthly light availability and soil moisture measurements, I combined monthly measurements into early (January and February) and late (March and April) growing season availability, for a total of six resource variables (resin available N, early and late season light availability and early and late season soil moisture, aboveground biomass). I applied a "varimax" rotation to the first two principal components to facilitate the interpretation of the gradients of resource availability.

Phytometers

To assess how phytometer growth and fitness differed within the two communities and along the resource gradient, we again used the proc mixed module within SAS (version 9.3). For each species I conducted a three-way ANOVA, with community type and N treatment as main factors and light treatment as a split-plot factor. Block was included as a random effect and denominator degrees of freedom were adjusted to reflect the split-plot factor, using a Sattherthwaite approximation. For *Avena*, spikelet production was used as an estimate of fitness, and for *Stipa,* survivorship was used. These data were log transformed and arc-sine transformed to meet assumptions of normality, respectively. Because of the differences in life histories of these two species, I was not able to directly compare the invader and resident fitness to assess if there were relative fitness differences that contributed to either invasion or invasion resistance. Instead I inferred these dynamics, using evidence for negative frequency dependence (i.e., fitness was greater in heterospecific community compared to conspecific), where the presence of negative frequency dependence would infer niche differences and coexistence and the lack thereof would indicate potential positive feedbacks contributing to invasion resistance. To account for the additional recruitment filter for *Stipa* (i.e. summer survivorship of the perennial seedlings), I ran two additional models for *Stipa* phytometers: 1) a three-way anova as described above and 2) a backwise selection logistic regression using end of the growing season soil moisture, community type and size as potential predictors of summer survivorship and AIC scores to compare models within the "lme4" package in R (version 2.15.1; Bates et al. 2011). I hypothesize that 1) the native perennial and exotic annual grass will coexist if they are able to maintain a higher fitness or establishment success in the heterospecific community under ambient resources, 2) increased N will facilitate invasion, if the exotic annual is able to increase its fitness under high N within the perennial community, and 3) increased N will enhance species dominance as a result of an interactive effect of species effects and N availability, if fitness or establishment success of the 'invader' differed between the two communities under similar environmental conditions (note: here I use the term 'invader' to refer to a species entering a community at low abundance regardless of its origin).

To tease apart the effects of species and resource availability on phytometer fitness, I conducted an ANCOVA where for each species I regressed the PCA axes scores against spikelet number for *Avena* and survivorship for *Stipa* by community type using the "nlme" package within R (Pinheiro et al. 2013). A significant effect of community type would suggest that there are additional species effects independent of resources that are affecting either fitness or survivorship and a significant interaction of community type and a PCA axis would indicate the presence of either a negative or positive feedback.

Results

Resource Availability

Resin available N was the greatest in the high N treatment but did not differ between the low N and control treatments ($F_{2, 24}=12.50$, $P<0.001$) and did not differ across species or light treatments ($F_{1,24}=0.30$, $P=0.59$; $F_{2, 48}=0.01$, $P=0.99$, respectively). Soil moisture was greatest in February for all N treatments, decreased throughout the rest of the growing season ($F_{3, 144}=256.7$ $P<0.0001$) and was lowest in high N plots at the end of the growing season (NxTime $F_{6, 144}=15.24$, $P<0.001$). Soil moisture did not vary across the light manipulations ($F_{2, 48}=1.15$, $P=0.32$) but was lower in high N plots regardless of species type ($F_{2, 24}=52.45$, $P<0.0001$). Finally, soil moisture did not vary between the *Stipa* and *Avena* plots ($F_{1, 24}=0.53$, $P=0.47$).

Aboveground plot biomass was greater within *Stipa* plots compared to *Avena* (424.7 $g*m^{-2}$ vs 213.6 $g*m^{-2}$, $F_{1, 24}=9.73$, $P<0.005$) and increased along the N treatments ($F_{2, 24}=45.21$, $P<0.001$). Biomass decreased the most in the annual low N plots (Type*N, $F_{2, 24}=15.60$, $P<0.001$) but did not vary across the light treatments ($F_{2, 48}=1.67$, $P=0.20$). The first principal component described the availability of N and soil moisture within the plots such that soil moisture decreased as resin available N and plot biomass increased across this axis; it described 32.2% of the variation in the resource dataset (Figure 1).

Light availability was greater in the perennial *Stipa* neighborhood compared to the annual *Avena* ($F_{1, 24}=61.45$, $P<0.0001$) and lower in the high N plots compared to the low N and ambient N plots ($F_{2, 24}=13.36$, $P<0.0001$). Light availability did vary according to my light manipulations ($F_{2, 48}=110.8$, $P<0.0001$). Although light availability tended to increase over the growing season across all the plots ($F_{3,144}=15.17$, $P<0.0001$), mean light availability did not differ over the growing season within the *Stipa* plots (Type*Time, $F_{3,144}=25.63$, $P<0.001$). Light availability over the growing season varied differently within the N treatments, where it increased over time in the low and ambient N plots but did not change within the high N plots (Nitrogen*Time, $F_{6,144}=16.16$, $P<0.001$). Early and late season light availability was described by the second principal component and described an additional 30.8% of the variation in the resource dataset (Figure 1).

Annual Phytometers

Avena phytometers were five times larger in *Stipa* plots compared to *Avena* plots ($F_{1,24}=37.37$, $P<0.0001$) and increased in size along the N gradient (0.39g, 0.62g, 1.58 g, respectively; $F_{2,24}=8.76$, $P<0.0027$). Moreover, these phytometers were on average 20 times larger in high N, *Stipa* plots compared to ambient N *Avena* plots (6.05g vs 0.28g, respectively; Type*N $F_{2,24}=3.52$, $P<0.05$).

Average fitness (i.e. spikelet production) of an *Avena* phytometer was greater in *Stipa* compared to *Avena* plots (17.6 vs 3.5 spikelets, respectively; $F_{1,24}=46.40$, $P<0.0001$). *Avena*'s average fitness also increased with N (4.5, 7.1, 15.1 spikelets, respectively, $F_{2,24}=4.17$, $P=0.03$) . Nitrogen addition tripled the fitness of *Avena* phytometers in *Stipa* communities but did not affect the average fitness of *Avena* within *Avena* communities (Figure 2, Type*N $F_{2,24}$=4.17, P<0.05). *Avena* phytometer weight was similar between high and low light plots and was larger in both of these plots compared to the ambient light plots ($F_{2,48}$=3.30, P<0.05;); *Avena* fitness followed the same trend as *Avena* weight within the light manipulations ($F_{2,48}$=4.22, P=0.02).

Avena fitness decreased along PC1 as N availability and plot biomass decreased and soil moisture increased and it decreased more sharply within *Stipa* neighborhoods (PC1: $F_{1,86}$=35.98, P<0.001; PC1*Type:$F_{1,86}$=12.49, P<0.001; Figure 4a). *Avena* fitness similarly decreased along PC2 as light availability increased (PC2: $F_{1,86}$=6.60, P<0.05; PC2*Type:$F_{1,86}$=3.56, P=0.06; Figure 4b).

Perennial Phytometers

Survivorship of *Stipa* seedlings at the end of the growing season was greater in *Stipa* plots regardless of N level (Type: $F_{1,24}$=53.42, P<0.000;1 Figure 3a). Within *Avena* plots, *Stipa* survivorship decreased as N availability increased (Figure 3a; Type*N: $F_{2,24}$=9.84, P<0.001). The mean weight of a surviving *Stipa* phytometer at the end of the first growing season was less than 0.10g; however, individuals were still larger in *Stipa* plots compared to *Avena* (0.044g vs 0.015g, respectively; $F_{1,24.2}$=51.38, P<0.0001). While biomass for an individual tended to increase with N, it was greatest in ambient and high N *Stipa* plots (N: $F_{2,24.1}$=3.02, P<0.07; Type*N $F_{1,24}$=15.07, P<0.0001). *Stipa* biomass did not differ among the light treatments ($F_{2,45}$=0.37, P=0.69). *Stipa* phytometer survivorship decreased over the summer within both neighborhoods. While summer survivorship was greater in *Stipa* compared to *Avena* plots, it did not vary within *Stipa* plots along the N gradient (Figure 3b; Type: $F_{1,24.3}$=0.5.09, P=0.03 ; N*Type: $F_{2,24.3}$=8.90, P=0.001). Conversely, within *Avena* plots *Stipa* survivorship increased as N level decreased (Figure 3b: N*Type: $F_{2,24.3}$=8.90, P=0.001).

Stipa survivorship increased within both neighborhoods as soil moisture increased and soil N and plot biomass decreased and similarly with increased light availability (PC1: $F_{1,86}$=8.91, P<0.01; PC2: $F_{1,86}$=44.45, P<0.001) but this relationship was stronger within *Avena* plots (PC1*Type:$F_{1,86}$=6.16, P<0.02; PC2*Type:$F_{1,86}$=4.9, P=0.03; Figure 4c, d, respectively). Though growth over the first growing season alone did not predict summer survivorship (z=-0.802, P=0.42), summer survivorship was dependent on neighborhood and soil moisture such that survivorship was greater in perennial plots and increased with April soil moisture (Type: z=3.69, P<0.001;SM: z=3.71, P<0.001); however the importance of soil moisture to summer survivorship was dependent on neighborhood (SM*Type: z=-3.93, P<0.001,Table 1).

Discussion

As environmental change alters the timing and availability of resources, it is changing the niche and fitness differences that promote coexistence (HilleRisLambers et al. 2012). Within this study I observed that increased Nitrogen (N) availability altered the fitness of both the native perennial *Stipa* and the exotic annual *Avena* to promote the invasion of the native community and enhance the dominance of the exotic community. These results support the observed pattern of an increase in annual species under N enrichment and further support the hypothesis that increased soil N levels will promote plant invasions (Vitousek et al. 1997a, Suding et al. 2005, Cleland et al. 2011). Morever, the dependency of native and exotic establishment on starting conditions suggests that species impacts that result in priority effects as well as resource availability can play an important role in predicitng responses to environmental change (Abraham et al. 2009).

Empirical studies are an important component of improving our understanding of the extent that environmental change is affecting the mechanisms that promote species coexistence and diversity. My approach allowed me to explore how the differences in inter- and intraspecific interactions can contribute to observed species coexistence by focusing not solely on the growth of individuals but on an individual's fitness. For the exotic annual, I observed that it had greater per capita fitness within the native perennial monoculture, compared to a monoculture of its own species (Figure 3). This negative frequency dependence for the exotic annual suggests that within the native perennial population at low and ambient resource conditions, niche partitioning would likely promote coexistence between *Stipa* and *Avena,* as hypothesized*.* While I was not able to follow these populations until they reached a new equilibrium state to confirm coexistence, these results support the abundance patterns found in other studies where an exotic annual is able to persist within a native *Stipa pulchra* stand (Seabloom et al. 2003b, Corbin and D'Antonio 2004b).

Integrating the impact that a species has on its environment is key to improving our understanding of how environmental change can shift species interactions and ultimately change community composition. Frequency dependent species impacts on N availability have conferred dominance in many perennial dominated herbaceous systems, where we are already observing compositional shifts due to N enrichment (Wedin and Tilman 1990, Suding et al. 2005). I found evidence for these positive feedbacks within the perennial *Stipa* plots, as its survivorship was greater within its own plots; while I did not observe strong effects of the Stipa on N availability, *Stipa* had strong impacts on light availability within its plots. Ultimately, however, it is unlikely that this positive feedback would confer invasion resistance for the perennial community under high N scenarios. The large increase in *Avena*'s fitness under high N in the *Stipa* plots is indicative of a change in the relative fitness differences of the two species, which would favor the population growth and invasion of the exotic (Huenneke et al. 1990, MacDougall et al. 2009).

Results from this study can also be applied to question whether *Stipa* populations could re-invade invaded areas, given sufficient propagule pressure. Here, I found little evidence to expect this natural colonization, particularly at high N. The low survivorship of the native *Stipa* under ambient and high nitrogen conditions suggests that the exotic annual has altered the environment to promote its own growth. This positive feedback was stronger under high N conditions as almost no perennial seedlings were able to establish in these plot, supporting the idea that exotic plants can form persistent communities(Kulmatiski 2006); however a longer term study would be needed to fully evaluate their stablility. Morever, these dynamics suggest that as nitrogen levels increase with atmospheric deposition, native communities may be more susceptible to invasions after a disturbance, as the exotic annuals may be able to reach more quickly the frequency needed to exhibit positive feedback dynamics (MacDougall and Turkington 2005, Kulmatiski 2006).

Is the poor native perennial establishment within the exotic annual community solely due to a shift in limiting resources (i.e. a shift from nitrogen to light limitation) as theory predicts? The native perennial's mean survivorship and growth did not vary across the light manipulations, which is likely due to the fact that the light availability at the beginning of the growing season, while different between the two species, did not differ between some of the light treatments (i.e. light availability was similar between the ambient and high light perennial plots and between the ambient and low light annual plots). The principal components analysis, however, did show that perennial survivorship increased with increasing light availability within the exotic annual plots, as predicted (Figure 4d, solid line). However my experimental manipulations allowed me to separate the natural inverse relationship of nitrogen and light availability. This approach revealed that under low nitrogen conditions regardless of light availability, the perennial *Stipa* was able to more successfully survive the first growing season and additionally the summer (Figure 4a,b). These results suggest that even though light availability may improve survivorship, belowground competition for resources may be more strongly limiting recruitment of native perennials into these exotic annual dominated systems (Rajaniemi et al. 2003).

While species effects likely influence belowground competitive interactions in this system, effects on factors other than resources may also be involved. For instance, even when I simulated low light availability and high nitrogen availability within the native population, *Stipa* seedling survivorship was still greater compared to the similar resource environment in the *Avena* plots, suggesting that the perennial *Stipa* may be altering dynamics other than resources to improve its survivorship. While I was not able to explore these dynamics within this experiment, plant-fungal feedbacks have been shown to improve native species colonization within California grasslands (Vogelsang and Bever 2009).

Establishing within a Mediterranean climate for a perennial species means being able to survive the summer heat and drought. Tracking individuals through this additional filter revealed another important resource trade-off - that of soil nitrogen and soil moisture availability (Figure 1, axis 1). I found that summer survivorship for *Stipa* seedlings increased with soil moisture at the end of the growing season, and soil moisture was the lowest in high N plots at the end of the growing season (Table 1). Exotic annual grasslands have been shown to utilize and deplete soil moisture more rapidly during the early growing season and this may be intensified under high N conditions such as those created by atmospheric N deposition (Holmes and Rice 1996). This altered resource use pattern may leave perennial seedlings more vulnerable to summer mortality, as I observed here. This summer recruitment filter may become more critical for native perennial restoration efforts within California, as future precipitation patterns may interact with amtospheric deposition rates to influence exotic annual ecosystem level responses to higher nitrogen availability (Harpole et al. 2007).

Although these results are based on a short term study, I found strong evidence of species impacts that lead to positive feedbacks for both the native perennial and exotic annual. However these dynamics would likely only translate to invasion resistance for the exotic annual particularly under high N scenarios. The increase in fitness of the exotic annual within the native perennial under high nitrogen is evidence that an invader can interact with environmental change drivers, increased N levels in this case, to shift dynamics from coexistence to invasion (Didham et al. 2005). I did find evidence to support the prevalent management strategy of ammending soil nitrogen levels, as the native perennial had higher survivorship within the exotic annual community under the low nitrogen manipulation; however the higher summer perennial survivorship within these plots indicates that the success of this strategy is not solely due to an altered competitive environment for soil nitrogen but due to its indirect effects on soil moisture. Disentangling the contribution that species impacts may have on resources and subsequently species fitness will be key to understanding how species will respond to environmental change and how invaders may interact with this change to shift communities from invasion resistance or coexistence to invasion. Furthermore, understanding how environmental change may interact with invader impacts will be important to implementing successful restoration strategies.

Table 1. Summary of factors important to *Stipa* phytometers' summer survivorship. Results shown are from a generalized liner model fit by the Laplace approximation with Binomial errors. Subplot and Block were included as random effects.

Fixed Effects	**Estimate**	**Z value**
Intercept	-4.718 ± 2.25	-2.10*
Weight (log-transformed)	-0.377 ± 0.47	-0.80
Soil Moisture-April	0.279 ± 0.08	3.71***
Neighborhood Type	3.919 ± 1.06	3.69***
Weight : Soil Moisture	0.037 ± 0.02	3.37*
Soil Moisture : Type	-0.132 ± .03	-3.93***

* p-value = 0.01, *** p-value<0.0001

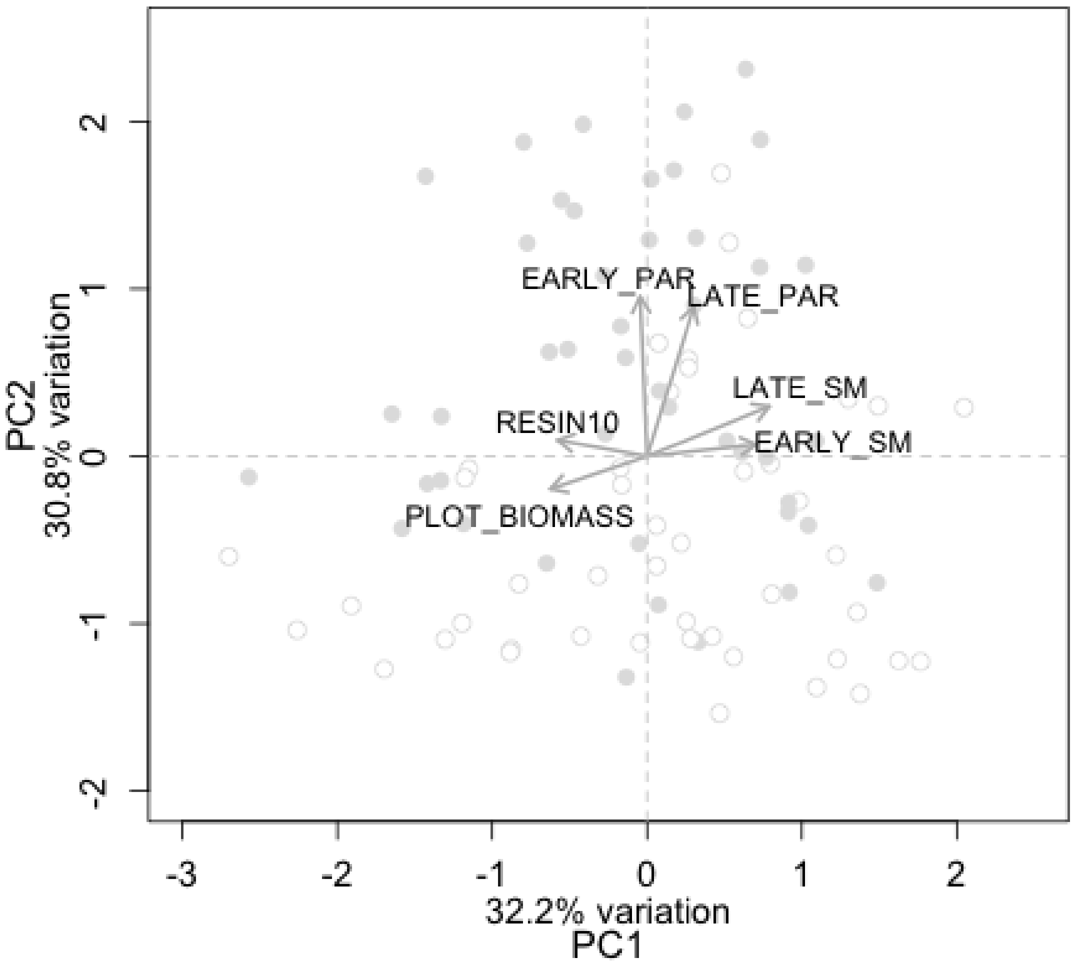


Figure 1. Biplot from rotated PCA ordination of the relationship among seasonal resource availability within plots. Principal components 1 and 2 explain 32.2% and 30.8% of the total variation in resources among the plots. Early and late are means for January and February or March and April, respectively. SM = soil moisture, PAR= light availability, Resin= resin available Nitrogen, Plot_biomass= aboveground biomass per m^2. Filled circles represent the native perennial *Stipa* plots and open circles represent the exotic annual *Avena* plots.

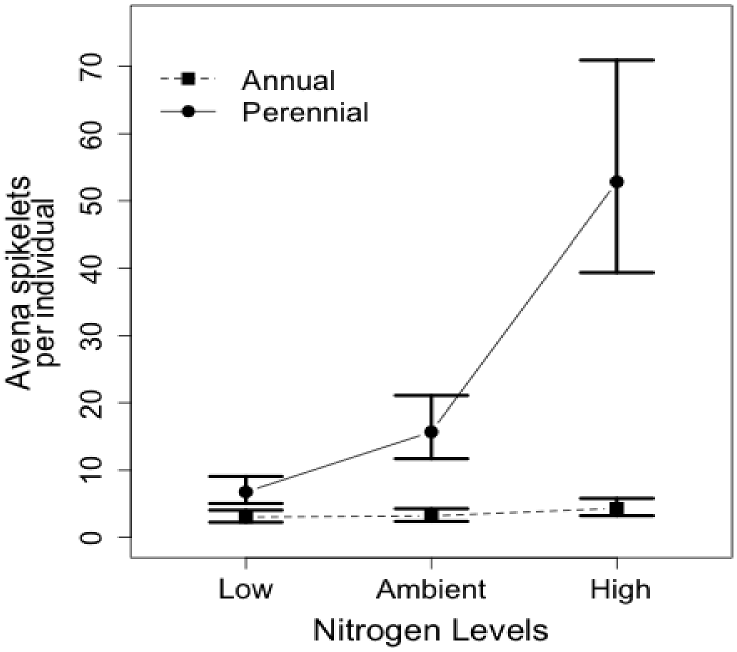


Figure 2. Fitness of exotic annual grass (*Avena fatua*) in annual (Avena, squares) and perennial (*Stipa*, circles) communities along a N gradient. *Avena* fitness was 15 times greater in perennial communities under high N compared to all other treatment combinations. *Avena* fitness was similar along the N gradient in the annual community type. Means ± 1 SE and are log back-transformed LSmeans.

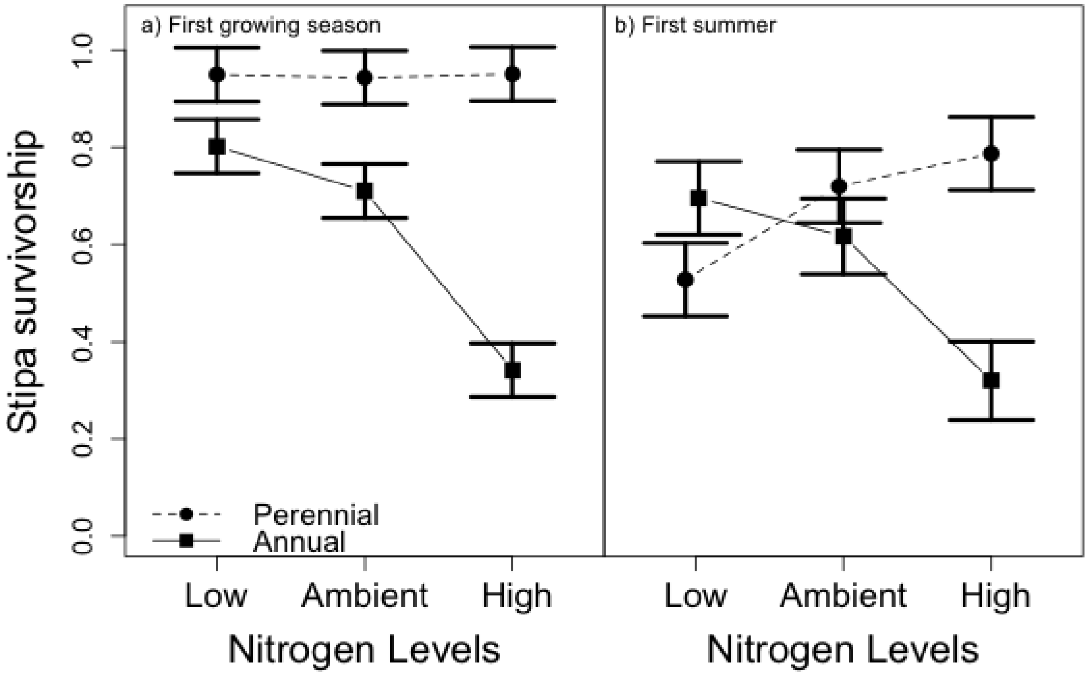


Figure 3. Survivorship of perennial grass (*Stipa pulchra*) in perennial (*Stipa*, circles) and annual (*Avena*, squares) communities along a nitrogen (N) gradient. Survivorship was highest during the growing season in perennial community types regardless of N level (a, dashed line) but lowest under high N in the annual community type (a, solid line). Summer survivorship in the perennial community type was lowest under low N (b, dashed line) but tended to be higher under low N in the annual community type (b, solid line). Values are LSmeans ± 1 SE.

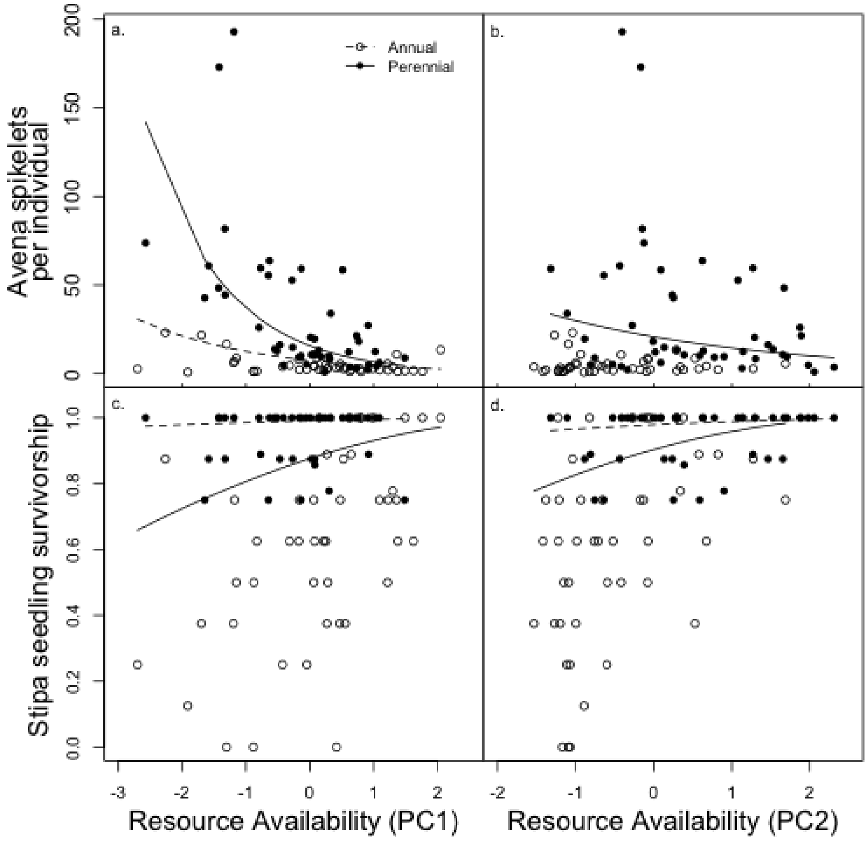


Figure 4. Relationship between the annual grass phytometer fitness (a, b) and perennial grass phytometer survivorship (c,d) and seasonal resource availability during the growing season, where high PC1 values indicate high soil moisture but low nitrogen availability and aboveground biomass and high PC2 values describe higher light availability. Fitness for the annual grass decreased along both resource axes (PC1:r^2=0.56, PC2:r^2=0.41), but decreased more within perennial community types (filled circles; PC1*Type: p-value<0.001; PC2*Type: p-value=0.06). Survivorship for the perennial phytometers increased with soil moisture (PC1, r^2=0.51) and with light availability (PC2, r^2=0.47) but increased more within the annual community (open circles; PC1*Type: p-value<0.02; PC2*Type: p-value=0.03). Lines represent back transformed log linear relationships for 'a' and 'b' and back transformed arcsine relationships for 'c' and 'd'.

Chapter 4

Effect of propagule pressure on recovery of a California grassland after an extreme disturbance

Introduction

Disturbances play an important role in shaping communities and ecosystems (Jentsch 2007, Fukami and Nakajima 2011). Large-scale disturbances can initiate successional dynamics, ensuring the persistence of many species via the subsequent stages of recolonization (Clements 1916, Connell 1978) and enhancing diversity at the landscape scale (Collins 1990, Cook et al. 2005). These dynamics are particularly critical in invaded landscapes of conservation concern (Buckley et al. 2007), as these same disturbances can provide windows of opportunities for invasion of exotic species, whose subsequent effects may shift the successional trajectory (Hobbs and Huenneke 1992, Huston 2004, MacDougall and Turkington 2005). These interactions will likely become even more critical as the frequency of extreme climate events (e.g., floods, drought) increases (Turner 2010). To effectively manage resilience to these future disturbances, it is important to understand the complexity of disturbance regimes and their ecological impact (Mori 2011). An integral part of this is understanding the relative responses of species within a landscape to disturbance (D'Antonio et al. 2001).

Initial recovery after a disturbance commonly depends on the species present prior to a disturbance leaving residual individuals, either vegetatively or in the seed bank (Noble and Slatyer 1980, Turner et al. 1998, Meiners et al. 2002). Residuals from the seed bank are often dominated by annual species that grow faster than perennial species growing from seed (Cook et al. 2005); however, residual perennial plants can reestablish vegetatively after a disturbance and achieve large sizes more quickly than those that start from seed (Gleeson and Tilman 1994). In cases where natives and exotics differ in life history, this balance of residual components (vegetative, seed bank) is thought to influence interactions between native and exotic species during the “invasion window” following a disturbance (Meiners 2007, Tognetti et al. 2010) and to result in a classic competition-colonization tradeoff (Levins and Culver 1971). While these tradeoffs could strongly influence invasion dynamics, there have been few explicit tests (but see Keeley et al. 2005).

Our understanding of how interactions between species characteristics and propagule pressure impact invasion success following a disturbance is limited (Zouhar et al. 2008). Propagule pressure, either from residual plants or new colonists from surrounding patches, can strongly influence post-disturbance regeneration and invasion success (Lockwood et al. 2005, Colautti et al. 2006). While dispersal from surrounding intact communities can influence recovery of an area after disturbance (Connell and Slatyer 1977), large disturbances can isolate areas and initiate within these isolated areas nucleation processes as residuals either vegetative or from the seed bank become the foci for colonization and expansion of populations (Zobel et al. 1993, Turner et al. 1998). Recovery of the native species in a patch can stall if recovering neighboring patches are dominated by exotics with high dispersal capabilities that colonize the native patch before the native patch is able to recover (Moody and Mack 1988, D'Antonio et al. 2001, Platt and Connell 2003).

Here, I investigate how propagule pressure influences invasion following an extreme disturbance (an intense fire following a record drought). I focus on a situation common in invasion, where exotics and natives differ in both their regeneration strategies and dispersal abilities, and investigate how these differences may alter early successional dynamics in a patchy, invaded landscape (Cook et al. 2005, Meiners 2007). I predict that, if the exotic annual is able to disperse into and establish within the native patches, the colonization window following a disturbance should result in a homogenization of the landscape over time towards exotic annual dominance. In contrast, if dispersal among patches is limited, both native and exotic patches should be maintained in the landscape as local competition dynamics determined by residual individuals (both vegetative and seedbank) would determine recovery (Figure 1).

Throughout California large portions of native grasslands have been invaded by exotic annual grasses from the Mediterranean (Heady 1977). Traditionally this invasion is thought to be a result of the exotic grasses competitive advantage over the native grasses (Dyer and Rice 1997, 1999); however recent research within California suggests that these invaders may be the ‘passengers’ not the ‘drivers’ of change (HilleRisLambers et al. 2010). If disturbance does favor these invaders then understanding the mechanisms by which the invader is able to capitalize during recovery is important for management (Firn et al. 2008). Furthermore, weather perturbations, such as drought, can alter the intensity of a disturbance and the community’s response to the compounded events (Paine et al. 1998).

I focus on the effects of an extreme disturbance -- a record drought followed by a large-scale fire -- on a patchy, invaded grassland landscape in California. The goal of this study was to evaluate 1) the temporal pattern of native perennial and exotic annual grassland recovery after the disturbance and 2) how landscape (i.e. propagule pressure) dynamics following disturbance contribute to the recovery of native grasslands or the spread of exotic annuals.

Methods

Study Site

I conducted this study at Loma Ridge in Irvine, California within the Irvine Ranch Land Reserve (N:33.7501 W:-117.71787). The climate is Mediterranean with a growing season from November to June as determined by rainfall (e.g., the 2010 growing season was from November 2009 to June 2010). Average growing season rainfall from 1991-2010 was 330 mm and average growing season temperature over the same period was 20.9°C. Annual precipitation over the course of the study (2007-2010) was 68, 211, 214, and 175 mm, respectively (California Irrigation Management Information Services, http://wwwcimis.water.ca.gov/cimis/welcome.jsp). The first growing season (November 2006-June 2007), just prior to the burn I studied (October 2007), was one of the driest years on record (Keeley et al. 2009).

Loma ridge is a topographically-complex site with a string of grassland vegetation on the ridge top and on north and west facing slopes, a steep erosional cliff on the southern edge, and coastal sage scrub vegetation to the north on south facing slopes. While variable, most of the grassland area was less than 0.3km in width, delimited by the cliff and sage scrub vegetation to either side. During the 2007 growing season (prior to the fire), I identified eight grassland sites each containing paired patches dominated by either native or exotic species. These eight sites were within 2km of each other along the ridge. Patches were designated by the dominance (>80% abundance) of the native perennial grass, *Stipa pulchra* Hitchc., or exotic annual grasses, *Avena fatua* L. and *Bromus diandrus* Roth, and were at least 20m^2 in size. I used paired patches to minimize possible differences in environmental characteristics, such as slope and aspect, and paired patches did not differ in soil texture (Larios unpublished data). A small two-track road provided access along the ridge but was limited to researchers and security patrols. At each of the eight sites, I set up two 1m^2 plots, randomly within each native and exotic patch (a total of 32 plots). Plots in paired patches within a site were 10-15 m apart, while plots within a patch were 2-5m apart.

All of these sites were burned in the 2007 arson-caused Santiago wildfire, which occurred from Oct 21 –Nov 4, 2007, and was the most disastrous fire in Orange County in over 30 years (OCFA 2008 , Figure 2). The fire was intense; it completely removed all aboveground vegetation and litter from the study site and in total burned 28,517 acres (OCFA 2008), leaving no unburned intact grassland communities within 5km. Due to the scale of the fire as well as the timing of the extreme drought, I focus on temporal dynamics of recovery following 2007. While I was not able to include comparison with areas that did not burn or experience the intense drought, observational evidence indicates that the patchy mosaic within the eight grassland sites had been present on Loma Ridge for at least a decade prior to the burn (T. Smith, personal communication).

Measurements

I measured aboveground biomass and species composition annually from 2007-2010 (the drought year prior and three years following the fire). Each year at peak biomass, I clipped all aboveground biomass at ground level within a 25x25cm subplot and sorted the biomass to species (nomenclature after Baldwin et al. 2012). Native perennial biomass was additionally sorted as either adult or seedling to distinguish between residual vegetation and newly colonizing vegetation. A subplot was never sampled twice. After sorting, samples were dried at 60^{o}C for 48 hours and weighed.

To estimate propagule pressure, I measured seed rain along transects that ran between paired native and exotic patches. I took these measurements in five additional sites that had also burned in the Santiago Fire and were adjacent to the sites where I measured species composition. At these five sites, I set up three 8m transects that extended from the center of a native patch, across the patch edge, and into the center of an exotic patch. To collect seed rain, I placed petridishes (8.5 cm in diameter) filled with sticky resin (Tanglefoot™, Conotech Enterprises, Canada) every 80cm along the 8m transect. I collected seed rain over the entire seed dispersal period the first year after the fire (April-October 2008), checking traps biweekly and replacing them once in July. I identified and counted all seeds within each trap using a reference seed collection. Additionally, I counted seedlings (stem counts) in a 25 x 25cm subplot at each of the above-mentioned sampling points, the following growing season (2009) to estimate how seed rain related to subsequent recruitment.

Analyses

To compare aboveground biomass and species richness over time between native and exotic patches, I used a linear mixed effects model with Patch Type and Year as fixed effects, and Site as a random factor. I additionally included precipitation as a continuous variable to account for interannual variability related to rainfall; however I did not include the 3-way interaction of Year, Type and Precipitation. When precipitation was not a significant variable, I dropped it from the analyses. For all analyses I averaged the values for the two plots within each patch and used R statistical software (version 2.15.0, RDevelopmentCoreTeam 2012). All linear mixed effect analyses were run using the "nlme" package (Pinheiro et al. 2011).

To evaluate the recovery of the native and exotic patch types (designated prior to the fire), I first grouped species into three abundance categories (dominants, subdominants, and rare) based on species rank abundance curves within each patch type (Grime 1998). Using the "BiodiversityR" package (Kindt and Coe 2005), I calculated a rank abundance curve within each patch for each year following the fire (2008-2010). I did not use abundance from 2007 to classify species groups as several of the less abundant species were notably absent due to the drought. I classified a species as "dominant" if it was present in a patch all three years with 20% or greater abundance each year. A subdominant was present with abundances between 1- 20% within any year. A rare species was present with a maximum abundance of 1%. Note that these groupings were based on rank abundance curves in exotic and native patches, not on the origin (exotic or native) of the species. To incorporate origin, these groupings were subdivided based on species origin (either native or exotic; Appendix 2). Using this classification, the perennial bunchgrass, *Stipa pulchra,* was the only native dominant, while three annual grasses (*Avena fatua, Bromus diandrus,* and *Festuca perenne*) comprised the exotic dominant grouping.

To assess recovery of the species groups, I ran a linear mixed effects model for each group with initial Patch Type (native or exotic) as a fixed effect, Year (2007-2010) as a continuous effect and Site as a random effect. I conducted post-hoc contrasts to compare groups when a significant interaction (Patch Type x Year) was present. There were many cases where a species group was frequently absent in a given patch type (e.g., native dominants in exotic patch type); therefore, to assess how the abundance of the native and exotic species groups shifted through time, within each patch type I additionally conducted a similar linear mixed model as described above but with species Origin (native or exotic) instead of Patch Type as a fixed effect. If a group still lacked adequate representation, I dropped the comparison that was lacking adequate representation. To account for the lack of independence between plots over time, I estimated effects based on maximum likelihood estimations (Everitt and Hothorn 2011).

To determine propagule pressure, I averaged seed rain at each distance among the three transects within each sampling site. We compared exotic (*Avena fatua, Bromus diandrus*, and *Festuca perenne*) and native (*Stipa pulchra)* seed rain within each distance with paired t-tests. To assess how this seed rain related to abundance the following growing season, I conducted a linear mixed effects model for the abundance of each of the native and exotic dominants with Seed Rain as a continuous factor, Block as a fixed factor, and Distance along the transect as a random factor.

Lastly, to determine the dependencies between abundances in paired patches within a site (i.e., a indicator of dispersal among patches), I calculated Bray-Curtis dissimilarity (Bray and Curtis 1957) between the paired native and exotic patches within each site using the species abundance groups. I compared dissimilarity over time using a linear mixed effects model with Year as a continuous factor and Site as a random effect. I interpreted a decrease in dissimilarity over time as evidence of homogenization across sites. I then examined three factors that could explain dissimilarity patterns across sites: average site aboveground biomass, species richness (i.e., the total number of species) and the abundance of exotic dominants establishing in native patches.

Results

Environment

Aboveground biomass was lowest during the drought year (29.34 g/m^2; 2007) and increased after the fire (607.67, 738.75, & 586.08 g/m^2; $F_{1,53}$=18.02, P<0.001). It also was greater in patches initially dominated by exotics compared to natives ($F_{1,53}$=4.44, P=0.04; Appendix 3a). Species richness increased over time (2.4 in 2007 to 4.7 in 2010; $F_{1,53}$=13.07, P<0.001) and was significantly greater in the native patches than exotic patches in 2009 & 2010 (Year X Type interaction, $F_{1,53}$=6.81, P=0.01, Appendix 3b). Precipitation did not consistently influence aboveground biomass or species richness ($F_{1,50}$=1.76, P=0.19 and $F_{1,50}$=0.65, P=0.43); however, the low precipitation in 2007 was likely responsible for the very low biomass and low richness (particularly in the native patches) during this year.

Response of Native and Exotic Dominant Species

Following the drought and fire, abundance of the dominant species in native patches changed with exotics invading native patches (Table 1, Figure 3). However, the exotic dominants maintained high abundances in the exotic patch type in each of the three years after the disturbance. In the native patch type, exotics increased from less than 2% abundance during the drought year to 25% the year after the fire, and reached 80% two years after the fire. The native dominant, *Stipa pulchra*, was absent from all but one exotic patch. In the native patches, *Stipa* abundance decreased from almost 100% prior to the fire, to 60% the year following the fire, to approximately 25% in the subsequent years (Figure 3b). Additionally within the native patches, no *Stipa* seedlings were present in the drought year (2007) or the year right after the intense fire (2008); however, they made up 37% and 14% of the *Stipa* biomass in 2009 and 2010 (non-drought years two and three years after the fire), respectively.

By the second year after the fire, the abundances of exotic dominant grasses did not significantly differ between patches that they initially dominated and patches where *Stipa* initially dominated (Year x Type interaction, Table 1; Figure 3a,b), and by the second and third years after the fire (2009, 2010), exotic dominants were greater in abundance than *Stipa* even in the initially-designated native patch type (Origin x Year interaction, Table 1; Figure 3a).

The native dominant, *Stipa*, never produced more seed rain than the exotic dominant grasses, regardless of patch type. Within native patches where *Stipa* abundance was still averaging over 50%, seed rain was similar for both the native dominant and exotic dominants (t=0.49, P= 0.65 at 0m, the start of the transect in the native patch core; Figure 4a). The seed rain of the natives was also positively correlated with the density of native seedlings the following year (r^2=0.79; P<0.001; Figure 4b). In the exotic patch type, exotic dominant seed rain was approximately 28 times greater than seed rain from native dominants. The seed rain of the exotics positively correlated with density of exotics (stem counts) the following year (r^2=0.74, P<0.001; Figure 4b).

Response of Native and Exotic Subdominant Species

The abundance of subdominant species did not consistently shift after the disturbance within either community type. These species were similarly abundant (10% abundance) in native and exotic patches across all years except for the year following the fire where they increased in abundance in exotic patches (from 10% to almost 30%, Year x Type interaction, Table 1). The abundance of native subdominant species was variable within the native patches, and they were rarely present in the exotic patch types (Figure 3a,b).

Community Response

The paired native and exotic patches, while initially very different from one another, became less dissimilar (i.e., more similar) to each other after the disturbances ($F_{1,23}$=60.96, P<0.001; Figure 5). This decreased dissimilarity was positively correlated with the abundance of exotic dominants in the native patch type ($F_{1,21}$=124.70; P<0.001; Figure 5) and was not correlated with average site aboveground biomass or species richness (p=0.54, P=0.60, respectively).

Discussion

Recovery after a disturbance is often highly dependent on the presence of residuals (Turner et al. 1998). In this case, after a record drought followed by an intense arson-caused fire, the native perennial residuals did not translate to a recovery of the native community type as would be predicted by the classic competition-colonization tradeoff (Figure 1, solid lines). Instead I observed a homogenization of the landscape over time as the abundance of exotic dominants increased within the initially-native patches (Figure 1, dashed lines). While annual exotics were not abundant in the seedbank within the native patches immediately after this extreme disturbance, a large influx of exotic annual seed from the neighboring exotic annual patches occurred in the first year following the fire. This strong propagule pressure resulted in high recruitment of exotic annuals and possibly an increased competitive environment for native perennial seedlings in subsequent growing seasons. These results suggest that dispersal among patches is a strong mechanism governing recovery trajectories and can likely initiate 'replacement competition' dynamics between new propagules (*sensu* Yu and Wilson 2001).

Competition-colonization tradeoffs traditionally argue for the displacement of the inferior competitor/better colonizer over time (Levins and Culver 1971). However the superior competitor is often more susceptible to extinction following habitat loss because it is strongly recruitment limited (Tilman et al. 1994, Tilman et al. 1997). While I was not able to measure mortality rates of individual *Stipa* plants, it is possible that the fire immediately following a record drought led to a more intense and thus severe fire and caused higher mortality of *Stipa* individuals than would be expected by either the fire or drought alone. Bunchgrasses can continue burning after a fire has swept through an area making them vulnerable in a high intensity fire (Dyer 2003, Keeley et al. 2011).

Limited *in-situ* regeneration of the perennial grasses can create gaps of bare ground that could provide viable microsites for colonization by incoming propagules, increasing the relative importance of dispersal and subsequent recruitment for the recovery of the native community (Kotanen 1997, Paine et al. 1998). These "colonization windows" created by disturbances can increase the susceptibility of a community to invasion (D'Antonio et al.

2001). Within the exotic patches, I observed that seed rain the year after the fire (2008) was dominated by the annual exotic dominants, such that there was little native dominant seed input into the exotic patches. Conversely within native patches, I observed comparable seed rain for native and exotic dominants; however, this seed rain translated to double the recruitment of exotic annuals compared to native perennial seedings the subsequent year (2009) and a high abundance of exotic annuals the following year. Additionally, studies have shown the *Stipa* has a limited seedbank (Major and Pyott 1966, Cox and Allen 2008), and the lack of any *Stipa* seedlings during the first growing season after the fire suggests that the *Stipa* seedbank is likely susceptible to intense fires, which would limit the population's recovery to vegetative adults during the first year. While I was not able to fully isolate the effect of propagule pressure by experimentally manipulating seed inputs, these results support previous work showing limited seed dispersal and propagule pressure of the native perennials and high propagule pressure and dispersal ability of the exotic annuals (Seabloom et al. 2003b, DiVittorio et al. 2007, Seabloom 2011). Furthermore, these results support that the dominance of exotic annuals is the result of the highly fecund annuals being able to recover quickly after a disturbance and capitalize on the "colonization window" (Corbin and D'Antonio 2004b, HilleRisLambers et al. 2010).

Within 3 years after the drought and fire I observed the homogenization of these grassland patches. Evidence suggests that these trajectories will be maintained, as natural recovery of native perennials is rare and has only been shown consistently in California's coastal prairies (Hatch et al. 1999, Kotanen 2004). While I cannot attribute the cause of this homogenization to any single factor, I expect similar dynamics following events that cause large-scale mortality of the native perennial species.

Recruitment of native perennial seedlings is likely constrained by factors quite different than those maintaining resistance to invasion in established native perennial grasslands. While previous research within California has shown that the native perennial bunchgrass, *Stipa pulchra,* is a superior competitor to exotic annual grasses (Corbin and D'Antonio 2004b), the observed recruitment dynamics support previous research that native seedlings are unable to grow quickly enough to effectively compete against the exotic annual grasses and transition into adults (Dyer et al. 1996). This new competitive hierarchy is possible within stage-structured populations like that of a perennial bunchgrass, which have multiple growth stages (e.g., seed, seedling, and adult; Yu and Wilson 2001).

California's grassland species composition and biomass fluctuates with the variable rainfall in California (Pitt and Heady 1978) and as a result abiotic factors can be more important in determining grassland species composition than biotic factors (Jackson and Bartolome 2002). In 2007, biomass and species richness were lowest across both patch types, likely due to the severe drought during that growing season. Although I did not find precipitation was a good predictor of biomass and diversity over time, this is likely due to the fact that annual growing season rainfall did not vary much in the years following the fire.

Fire has been an integral part of California's grassland ecosystem (Reiner 2007); it can increase the fecundity and establishment of native perennial grasses like *Stipa pulchra* (Ahmed 1983, Langstroth 1991) and reduce the fecundity of invaders (DiTomaso et al. 1999) depending on the timing of the fire (Meyer and Schiffman 1999). Therefore, prescribed burns are often advocated as a tool to restore native grasslands (Menke 1992).

While I cannot conclude with certainty the relative importance of the drivers responsible for the dramatic changes I observed, it may be that large-scale wildfires may result in dynamics different than prescribed burns, particularly if they interact with weather perturbations.

Sequential disturbances acting upon a system can interact to produce synergies that can alter a community's response and resilience to a disturbance (Paine et al. 1998, Davies et al. 2009). Identifying when these interactions will occur and understanding the potential synergistic effects is critical for land management under continuing global change (Turner 2010). Southern California is predicted to experience more severe droughts (Bell et al. 2004, Hayhoe et al. 2004) and is already experiencing altered fire regimes due to increased human activity (Syphard et al. 2007). Understanding how native perennial grasslands respond to these combined disturbances will be important to their future management and conservation.

While disturbances can promote native communities in some cases, this work suggests that it is important to consider landscape context as well as its interaction to other disturbances or weather patterns. Moreover, a less-intense fire following a particularly wet year may have facilitated native expansion rather than the contraction. Native perennial recruitment is highly limited by seed availability (Seabloom et al. 2003b, Seabloom 2011) and can be easily thwarted by the rapid colonization of exotic annuals in invaded landscapes (Seabloom et al. 2003b). Understanding the relative importance of dispersal limitation on the recovery of the native species can have significant impacts on management efforts. Furthermore, management strategies to enhance vegetative regeneration of natives and decrease propagule pressure of exotics such as low intensity prescribed fires and to introduce native species via seed addition with consideration of weather patterns will be key in maintaining these remnant grasslands.

Table 1. Mixed effects model table summarizing how species relative abundance was influenced by year (2007-2010), initial patch type (native or exotic) or origin (native or exotic) and their interaction with year. Site was included as a random effect in all models.

	Year		Type		Year*Type	
Response Variables	F-value	P-value	F-value	P-value	F-value	P-value
Among Patches						
Exotic Dominants	$32.384_{1,53}$	**<0.001**	$51.291_{1,53}$	**<0.001**	$24.251_{1,53}$	**<0.001**
Native Dominants*						
Native Subdominants *						
Exotic Subdominants	$0.000_{1,53}$	0.99	$21.575_{1,53}$	**<0.001**	$4.328_{1,53}$	**0.04**
	Year		Origin		Year*Origin	
Within Native Patches						
Dominants	$0.068_{1,53}$	0.80	$0.135_{1,53}$	0.71	$100.29_{1,53}$	**<0.001**
Subdominants	$1.970_{1,53}$	0.16	0.432	0.51	0.430	0.51
Within Exotic Patches						
Dominants*						
Subdominants	$1.464_{1,53}$	0.23	$68.91_{1,53}$	**<0.001**	$1.464_{1,53}$	0.23

* models were not run because the group was not present within some patch types. Significant results in bold, numerator & denominator degrees of freedoms shown as subscripts.

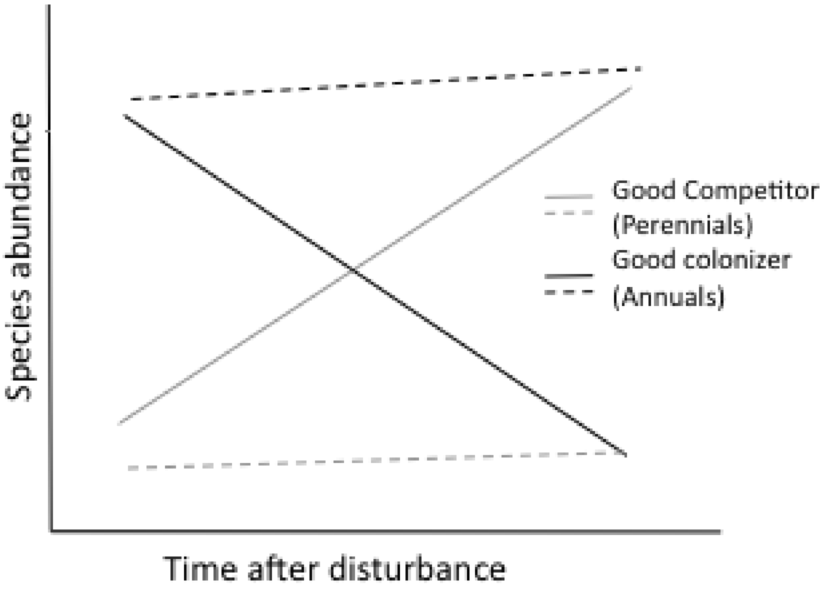


Figure 1. The relative influence of propagule pressure from neighboring invaded patches and survival of native residual individuals on the competition-colonization tradeoff following a disturbance. Scenario depicts invasion of a good colonizer (exotic annuals, in black) into patches dominated prior to the disturbance by the good competitor (native perennials, in gray). The expected competition-colonization tradeoff is shown in solid lines. With high propagule pressure and/or low residual survival (dashed lines), the expected tradeoff may not occur due to the strong propagule pressure of the colonizer and the strong dispersal limitation of the competitor.

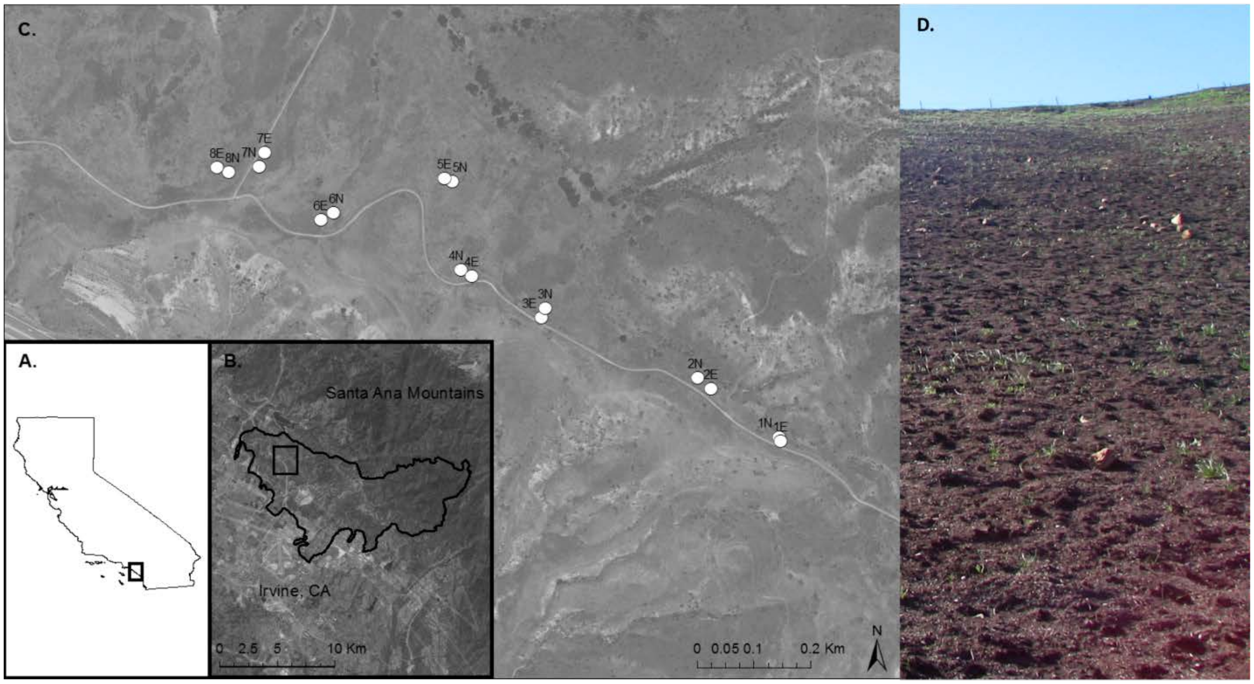


Figure 2. Map of paired native (N) and exotic (E) patches within 8 grassland sites in Irvine, CA. Inset ‘A’ shows the map of California with my study sites in the boxed area and ‘B’ shows the perimeter of the 2007 Santiago Wildfire and the rectangle within the perimeter highlights the location of the grassland sites. Across the ridge, the fire removed all aboveground vegetation (Inset ‘D’, photo credit: L. Larios).

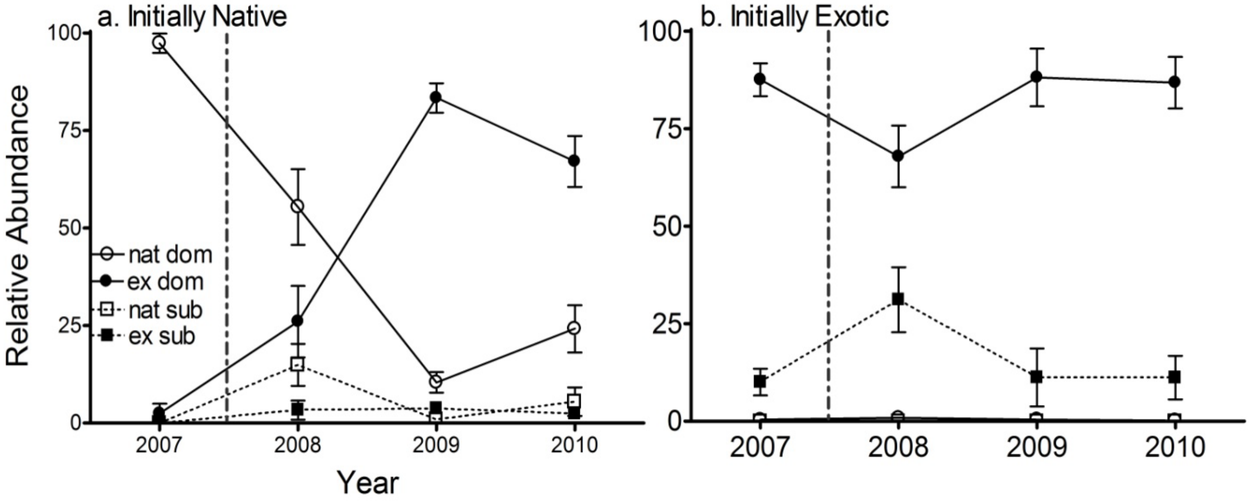


Figure 3. Relative abundance of species (means ± SEM) before and after fire (indicated by vertical dashed line; 2007 was a drought year) within initially native (a) and exotic (b) patch types. Species are grouped by origin (native, nat; exotic, ex) and abundance (dominant, dom; subdominant, sub). Within native patch types, dominance shifted from native to exotic species, while exotic dominants quickly recovered within exotic patches. Rare species are not shown. Specific species in each group are found in Appendix 2.

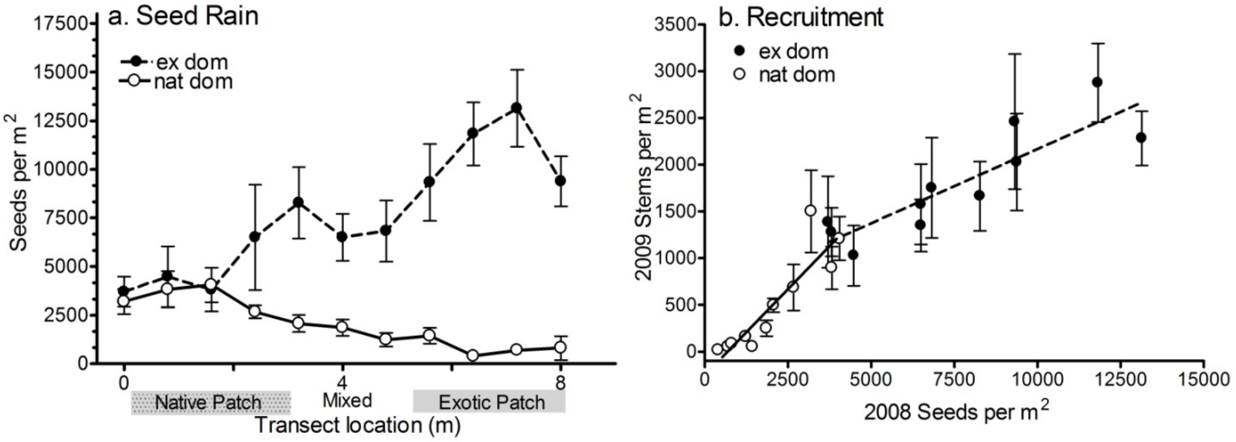


Figure 4. a) Seed rain of native and exotic dominants along an 8m transect bisecting native and exotic patches (n=5, for each point). While few native seeds made it to the interior of exotic patches, seed rain for the exotic (ex dom, filled circles) and native dominants (nat dom, open circles) was similar in the interior of the native patches. b) Seed rain of the exotic and native dominants was a strong predictor of recruitment the following year (n=5, for each point, lines represent significant relationships). For natives, because they are perennial, only seedling stem counts are reported. This distinction was not necessary for the exotics because they have an annual life history. Errors bars represent 1 SEM.

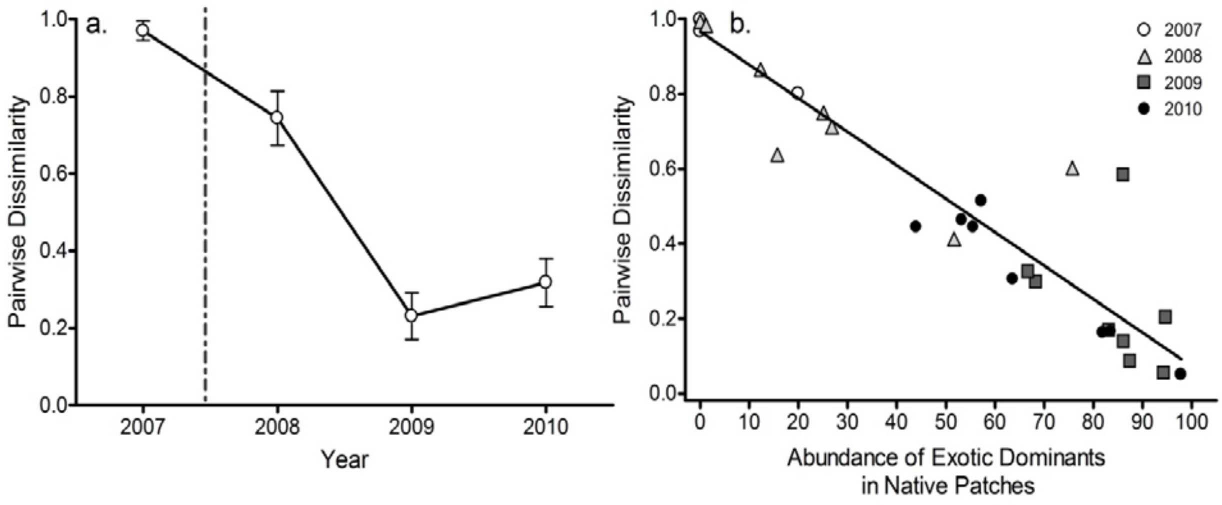


Figure 5. a) Pairwise (Bray-Curtis) dissimilarity between paired native and exotic patches (means ± SEM) within the eight grasslands sites over time (fire indicated by vertical dashed line). Pairwise dissimilarity was negatively related to the abundance of the exotic dominants establishing in the native patches (b).

Chapter 5

Changes in soil communities due to plant neighbors and soil resource availability alter native, *Stipa pulchra*, and exotic, *Avena fatua,* plant-soil feedbacks

Introduction

Increasingly the interactions between above and belowground communities are being identified as key determinants of the abundance and composition of plant communities (Wardle et al. 2004). While negative interactions are thought to be important in the maintenance of plant diversity (Klironomos 2002, Mangan et al. 2010), positive interactions can increase diversity in stressful environments (Bruno et al. 2003) and play key roles in ecological dynamics such as succession (Reynolds et al. 2003, van der Heijden 2004, Kardol et al. 2006) and invasions (Callaway et al. 2004, Suding et al. 2013). Several hypotheses attribute the success of exotics to their effects on the soil community by impacting beneficial soil biota for natives (Vogelsang and Bever 2009), allelopathy (Callaway et al. 2008), or accumulating pathogens that are detrimental to natives (Eppinga et al. 2006). These impacts all result in the exotic having a greater fitness in soils conditioned by itself compared to a native, and therefore a positive plant-soil feedback. However, there is still not a clear understanding of when and to what extent these plant-soil feedbacks may lead to recovery constraints or impede the efficacy of restoration efforts (Eviner and Hawkes 2008).

While widespread evidence indicates that soil microbial communities can be highly susceptible to changes in soil physical and chemical properties (Bissett et al. 2013), our understanding of how these shifts in microbial composition affect plant-soil feedbacks is limited. For example, increased soil nitrogen (N), via fertilization, atmospheric deposition or other anthropogenic inputs, can alter microbial composition towards a more bacterial dominated community and shift microbial-mediated ecosystem processes (Bardgett 1999, Allison 2002, Bradley et al. 2006, Zeglin et al. 2007). Low soil N availability found along natural gradients may have soil communities more dominated by fungal species (Bardgett and Shine 1999). Conversely, low soil N availability due to sucrose or sawdust addition can increase microbial activity, resulting in N immobilization (Blumenthal et al. 2003, Bleier and Jackson 2007, Sandel and Corbin 2010). While soil microbial communities from high N sites have been shown to differentially affect the growth of native and exotic species (Siguenza et al. 2006), it remains uncertain how changes in the microbial community as a result of changing soil resources may interact with any existing plant-soil feedbacks.

In addition to the physical and chemical properties of soil, host plant community composition can also play a significant role in dictating soil community composition (Bardgett and Cook 1998). Simply the presence of a neighbor, whether native or exotic, can alter soil microbial community composition via changes to soil resource availability via resource uptake or plant inputs (e.g., litter, exudates) into the soil (Bardgett 2002, Hausmann and Hawkes 2009). Thus, disentangling the relative contribution of soil resource availability and plant-plant interactions to changes in soil communities is key to understanding how plant-soil interactions may influence plant performance (Brandt et al. 2009).

Here I assess how plant-soil microbial feedbacks may change as soil microbial communities change with soil N availability and how these dynamics may be further altered by the presence of a neighboring plant species. I focus on California grassland, which has experienced a large-scale shift from native perennial grasses mixed with annual forbs to exotic annual grasses over the last century (Jackson 1985), as well as changes in atmospheric N deposition (Fenn et al. 2003). In this system, annual exotic grasses such as *Avena fatua* and *Bromus diandrus* foster species-specific soil microbial communities (Hawkes et al. 2005, Hawkes et al. 2006) and can alter the community of arbuscular mycorrhizal fungi (AMF) colonizing roots of native grasses such as *Stipa pulchra* (Hausmann and Hawkes 2009, 2010). Vogelsang and Bever (2009) showed that these impacts of exotic species on soil communities can reduce the growth of native species, consistent with the expectation that exotics experience positive feedbacks within their "home" soil AMF community.

While it has been well-documented that soil communities shift in the presence of exotic annual grasses, the contribution of this shift to invasion patterns depends on how the shift in soil communities occurs in the context of two other critical changes associated with invasion: changed soil resources and changed competitive interactions. Thus, here I assess the relative importance of changes in soil communities due to soil resources and plant-plant interactions on plant-soil feedbacks. I conducted a greenhouse experiment where I grew native *Stipa pulchra* Hitchc. and exotic *Avena fatua* L. in soils inoculated with conspecifics ('home') and heterospecifics ('away') soil communities. Soil inocula were collected from a restoration experiment (outlined in Chapter 5) where plots had been treated with either a carbon or nitrogen addition to affect soil resource availability. To examine the importance of plant-plant interactions, I grew plants individually or with a neighbor. If positive plant-soil feedbacks contributed to invasion, then *Avena* would grow better in its "home" soil than "away" soil communities; conversely if *Stipa* were to grow better in its "home" soil compared to "away", positive plant-soil feedbacks would prevent invasion. Soil resource effects on soil communities would contribute to invasion if *Avena* were to grow better with soil communities from high N sites. Plant-plant interactions would contribute to invasion if the presence of a competitor weakened the benefit that *Stipa* has when grown in its "home" soil communities.

Methods

Study species and soil

I focused on two species common to southern California grasslands: the native perennial *Stipa pulchra* Hitchc. and the exotic annual *Avena fatua* L. grasses (hereafter *Stipa* and *Avena*, respectively; nomenclature follows Baldwin et al. 2012). Soils for the experiment were collected from Loma Ridge in Irvine CA within the Irvine Ranch Land Reserve (N:33.7501 W:-117.71787) – a grassland largely dominated by a mixture of exotic annual grasses and native perennial grasses (Larios et al. In press). Background soil was collected from this site and upon collection the soil was air-dried, sieved through a 2mm sieve to remove rocks and debris and steam sterilized at 120°C. This soil was then mixed 1:1 with sterile coarse sand and used as the sterile background soil to fill 164 ml cone-tainers for the greenhouse experiment described below.

To test how changes in soil communities due to soil resource availability may alter plant performance, I collected soil inocula in March 2010 from a field experiment outlined in Chapter 6, where native and exotic plants had been grown in low, ambient and high soil N. Within each of the five experimental blocks, I collected soil from both the native and exotic plots. Within the native plots, soils were collected directly under a *Stipa* individual and for the exotics, under a stand of *Avena*, ensuring roots were collected with each soil sample. This soil was kept cool and shipped to the University of California Berkeley. Within three weeks of collection, the soils from each block were bulked to form the soil inocula used in the experiment. The inoculum was added to the cone-tainers at a ratio of 30 to 1, sterile background soil (described above) to inoculum (Bever 1994).

Experimental Design

To test the importance of plant-soil interactions in the absence of plant-plant interactions I planted three individual seeds of each species by themselves into conetainers with soil inoculated with either conspecific or heterospecific soil communities from low N, ambient, and high N sites. I additionally included a sterile soil treatment with no inoculum. Therefore, I had a total of seven soil-community treatments: *Stipa* conditioned 1) low N, 2) ambient N, 3) high N; *Avena*-conditioned 4) low N, 5) ambient N, 6) high N, and 7) sterile soil. To test the importance of plant-plant interactions on plant-soil interactions, I also planted species mixtures (consisting of one *Stipa*, one *Avena*) with the seven soil-community treatments described above. After initial germination I removed individuals from all conetainers so that each cone had a single individual for the no-competition *Stipa* and *Avena* treatments and two individuals for the competitive mixtures). I transplanted seedlings into the cones if no seeds germinated. The transplanted seedlings were planted at the same time as the other seeds so that they were comparable in size upon transplant. Thus I had a total of 420 conetainers (7 soil-community inocula x 3 species plantings x 10 blocks x 2 replicates within each block).

The plants were grown at the Oxford Tract Greenhouse at the University of California, Berkeley and were watered regularly with distilled water, without supplemental lighting or fertilizer. All above and belowground biomass was harvested 10 weeks after the initial planting. Transplanted individuals were harvested 10 weeks after transplanting. The biomass was sorted to species for the competition treatment, and all biomass was dried for 48 hrs at 60°C.

Statistical Analysis

To evaluate how plant growth varied across the experiment, I analyzed total biomass (sum of above and belowground biomass) with a three-way ANOVA model, specifying Block as a random factor, using the Proc Mixed module (SAS institute v 9.1).

I calculated the effect of the soil inoculum pairwise between the sterile soil treatment and the other soil inocula within each block with a response ratio: '$\ln(B_i/B_c)$', where B was the total biomass of the plant in either an inoculated soil treatments ('i') or sterile soil ('c'). I assessed the directionality of the response ratio using t-tests, where a value greater than 0 indicated a significant positive response and a value less than 0 indicated a significant negative response. To assess if the effect of simply adding soil inocula changed with culturing species or soil resource site, I ran a mixed effects model using the Proc Mixed module separately for each species with inoculum response ratio as the response variable, soil community sources (plant species, soil resource site) as two fixed factors, and Block as a random effect.

To assess if soil communities from varying soil resources affect plant performance, I calculated for each species a natural log response ratio (i.e. $\ln(B_{otherN}/B_{ambN})$), separately for the conspecific and heterospecific soil communities. I then analyzed this soil resource response ratio in a mixed model with soil community sources, species and soil resource site, as fixed effects and block as a random effect. A significant effect of soil resource for *Avena* would indicate that the changes in soil communities due to soil resources do alter performance, supporting my second hypothesis. A positive value would indicate the individual grew better in the altered soil communities, while a negative value would indicate it grew worse. A significant effect of the species soil inocula would indicate whether the effect of the soil resources varied between conspecific and heterospecific soil inocula.

Plant-soil feedback strength was calculated as '$\ln(B_{home}/B_{away})$', where B_{home} is the total biomass of an individual when grown in their conspecific soil communities, and B_{away} is the total biomass when grown in heterospecific soil communites. Plant-soil feedback strength was calculated within each soil resource community and competition treatment (i.e. *Avena* feedback for no-competition and low N would be the comparison of *Avena* biomass when grown alone, between conspecific (home) and heterospecific (away) cultured soils at low N sites). For blocks where individuals of a specific treatment died, I averaged biomass across the other blocks for that species as a substitute. I did this five times for *Stipa* when grown alone. For the competition treatments, I replaced the biomass of both the species nine times. However, I dropped any blocks that had lost replicates for three or more soil inocula treatments, resulting in a loss of one block for the no competition treatment and three for the competition treatments.

To assess how plant-soil feedback responses changed with competition or across the soil communities cultured from different soil N availability, I ran a mixed effects model with plant-soil feedback as the response variable and soil N inocula sources, species identity, and competition as fixed factors. Block was included as a random factor and any significant interactions were evaluated with post-hoc Tukey pairwise difference tests. A significant culturing species-target species interaction would indicate that plant-soil feedbacks could facilitate invasion, if *Avena* experienced no feedbacks when grown in "away" soil communities, but would indicate invasion resistance if *Stipa* experienced positive feedbacks when grown in "home" soil communities. A significant competition-species interaction would indicate that plant-soil feedbacks changed in the presence of a competitor, where a negative shift in feedbacks for Stipa when grown in competition would support my third hypothesis.

Results

Stipa pulchra response

Stipa total biomass varied as soil communities changed with culturing species and resource availability, where biomass was greatest in the conspecific, low N soil community and heterospecific high N soil community (culturing species x soil N interaction: $F_{2,76}=8.22$, $P<0.001$; Appendix 4). Competition decreased *Stipa* biomass by almost 90% (0.327g vs 0.036g, $F_{1,76}=595.9$, $P<0.0001$), and *Stipa* biomass was slightly greater when grown alone with conspecific soil communities compared to heterospecific, soil communities (0.386 vs 0.277g, respectively; Competition x culturing species interaction: $F_{1,76}=9.72$, $P<0.01$, Figure 1 square symbols).

Stipa grew better with sterile soil compared to heterospecific (*Avena*-cultured) soil communities and grew similarly between sterile soils and conspecific soil communities (Culturing species: $F_{1, 40}$=14.18 P<0.0001; soil N: $F_{2, 40}$=0.90 P=0.41; Figure 2a).

When grown alone, *Stipa* grew better with conspecific-cultured soil communities compared to heterospecific (better in home versus away soils), resulting in positive feedbacks when *Stipa* was grown alone (Figure 3a, dark gray bars). These positive feedbacks diminished when *Stipa* was grown with *Avena* (Spp x Comp, $F_{1, 76}$=7.45 P<0.01; Figure 3a light gray bars) and with high N soil communities (soil N x Spp, $F_{2, 76}$=6.24 P<0.01, low & amb N vs high N Tukey HSD P<0.01, P<0.05, respectively), resulting in the development of a strong negative feedback when in competition with *Avena* and in high N soil communities (Figure 3).

Soil resources altered soil communities such that *Stipa* grew better with soil communities from either low or high N availability compared to ambient N when soils were also cultured by the heterospecific, *Avena* (Culturing species: $F_{1,24}$=4.25, P=0.05, Spp x Soil N, $F_{1,24}$=0.95, P=0.33; Figure 4). Conversely changing soil resources within conspecific communities did not alter soil communities in a way that affected *Stipa* growth.

Avena fatua response

Avena exhibited little evidence of plant-soil feedbacks (Figure 3). The only exception to this pattern was a negative feedback at low N, where it grew worse in “home” low N soil communities (Soil N x Spp, low vs amb N: Tukey HSD, P<0.05). Interactions with *Stipa* did not alter *Avena* growth ($F_{1, 76}$=0.01, P=0.91; Figure 1 circles) nor change plant-soil feedbacks (Figure 3). Additionally *Avena* growth was greater in “away”, low N soil communities than in sterile soil conditions (Figure 2b, Culturing species x soil N: $F_{2, 40}$=3.36, P<0.05)

The soil resource environment of heterospecific soils did not alter the soil community in a way that altered *Avena* biomass; however, altering soil resources by increasing or reducing N in conspecifc plant communities resulted in soil communities where *Avena* grew worse compared to those under ambient resources (Spp source, $F_{1,24}$=10.22, P<0.01, Spp x soil N, $F_{1,24}$=1.45 P=0.23). Similar to *Stipa*’s response, *Avena*’s response to soil communities from altered soil resources was similar between the low and high N soil communities (soil N, $F_{1,24}$=1.45, P=0.23).

Discussion

Linking compositional shifts in soil microbial communities due to either changes in resource availability or host plant with plant-plant interactions is fundamental to understanding when plant-soil feedbacks (PSFs) play an important role in the maintenance of plant species diversity and in species invasions (Ehrenfeld et al. 2005, Bever et al. 2010, Suding et al. 2013). Here I observed that both soil resources and host plant can alter soil communities to create PSFs for both native *Stipa pulchra*, and exotic *Avena fatua;* however the directionality of these PSFs varied for the native and exotic.

Contrary to theory that predicts negative plant soil feedbacks within native communities (Reynolds et al. 2003), I observed that the native *Stipa* grew better with its home soil communities compared to the exotic *Avena* soil communities, resulting in positive feedbacks for *Stipa*. Additionally, *Stipa* grew worse with soil communities from *Avena*-cultured soils compared to sterile soil, suggesting that *Avena* is able to culture a distinct soil community that negatively affects the native, *Stipa.* On the other hand, in support for the hypothesis that exotic species experience either neutral or positive feedbacks in their introduced range (Reinhart and Callaway 2006, Inderjit and van der Putten 2010), I found that *Avena* grew similarly with soil conditioned by either conspecifics (*"Avena"* conditioned) or heterospecifics (*"Stipa"* conditioned). Similarly, Suding et al (2013) found this trend across pairwise feedback experiments of natives and exotics. While this result is consistent with several hypotheses that indicate that exotic species are able to alter soil communities to the detriment of natives (Eppinga et al. 2006, Callaway et al. 2008, Vogelsang and Bever 2009), this study does not allow me to identify by which mechanism this reduced growth occurs. Previously, Hausmann and Hawkes (2010) showed that a close congener of *Avena fatua*, *Avena barbata* exhibited strong effects on the soil fungal community, resulting in strong priority effects. These changes within the soil community may result in soil legacies that weaken native establishment success within invaded or previously invaded areas (Grman and Suding 2010).

As I hypothesized, soils conditioned under varying soil N resource availability negatively affected *Avena* growth, however only when *Avena* was grown in soils conditioned by itself. Unexpectedly, I found that the shifts in soil communities due to the changing resources in *Avena* conditioned soils improved the performance of *Stipa* when grown with *these heterospecific* soil inocula. Changing soil resource availability can shift the composition of soil communities from one dominated by bacteria at high nitrogen availability to one dominated by fungi at lower nitrogen availability. These compositional changes may alter plant performance depending on the strength of specificity on behalf of the microbes and host plant, where strong specificity for both microbes and plant host would result in a decrease in performance with composition shifts (Aldrich-Wolfe 2007, Lekberg et al. 2007). Within this experiment I found that the native, *Stipa,* did not respond to potential community shifts due to resources when grown with soil cultured by conspecifcs; however, I observed reduced growth by the exotic *Avena* when grown with its conspecific ("home") soil inocula cultured with different soil resources, supporting previous findings that *Stipa* has a broad AMF niche while *Avena* has a more restricted niche (Hausmann and Hawkes 2009). The beneficial affect that these compositional shifts in the *Avena* conditioned soil communities had on *Stipa* has interesting applications for native recovery management efforts. Soil N reduction activities are traditionally used to alter competitive interactions in favor of the natives (Blumenthal et al. 2003); however these results suggest that these soil N reductions may also minimize some of the negative effects that an exotic like *Avena* may have on the soil community.

In addition to *Stipa* biomass, competition strongly affected *Stipa*'s plant soil feedbacks, where the presence of *Avena* eliminated the positive effect that *Stipa*'s home soil had on *Stipa* growth. While this result is consistent with findings of resource competition between *Avena* and *Stipa* seedlings (Dyer and Rice 1997, 1999), this study does not allow me to decipher whether this result is also due to the strong control that *Avena* species may have on the soil community (Hausmann and Hawkes 2009). The strong effect of the *Avena* competitor on *Stipa* performance suggests that restoration efforts should continue to focus on ways to reduce the abundance of exotics in order to promote native species recovery.

In conclusion, I found that both plant host and soil resource availability effects on soil communities may alter plant growth. However, these effects strongly differ for a native and exotic and that competition disproportionately affected the native, *Stipa*. The native was more susceptible to host identity, where it grew less in *Avena* conditioned soils compared to sterile soil and conspecific conditioned soils. On the other hand, the exotic, *Avena* was more vulnerable to soil community shifts that resulted from changes in soil resource availability. Disentangling how soil resource availability as well as plant host may affect how soil communities affect plant performance is key to better understanding when plant soil feedbacks play a role in the spread and dominance of exotic species as well as plant community composition.

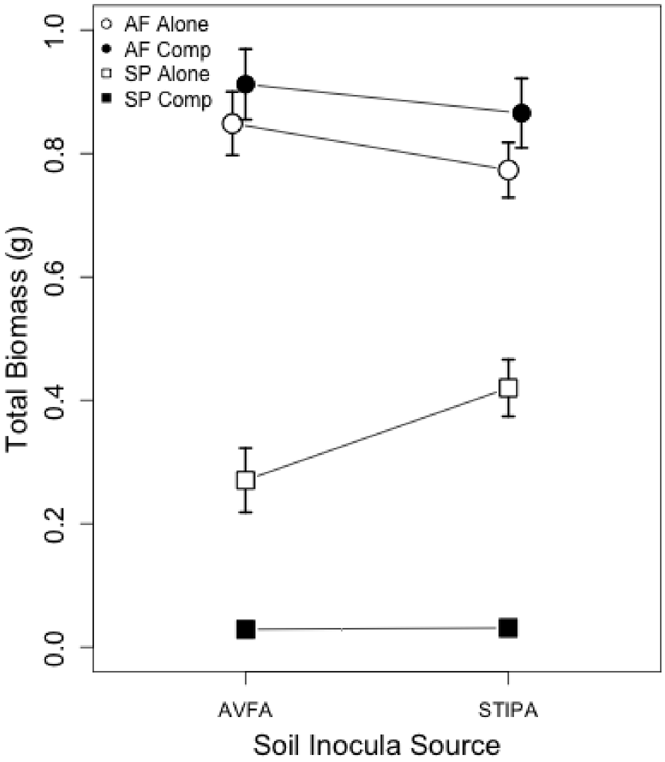


Figure 1. Total (above and belowground) biomass for *Stipa pulchra* (squares) and *Avena fatua* (circles) when grown alone (open symbols) or with a competitor (filled symbols) with soil inocula cultured under ambient resources by conspecifcs and heterospecifics. Competition decreased *Stipa* biomass, regardless in which soil community *Stipa* was grown. Avena grew similarly in both conspecific (*Stipa*) and heterospecific (*Avena*) soils regardless of the presence of a competitor. Mean ± 1SE. Error bars for *Stipa* with competitors are hidden by symbol.

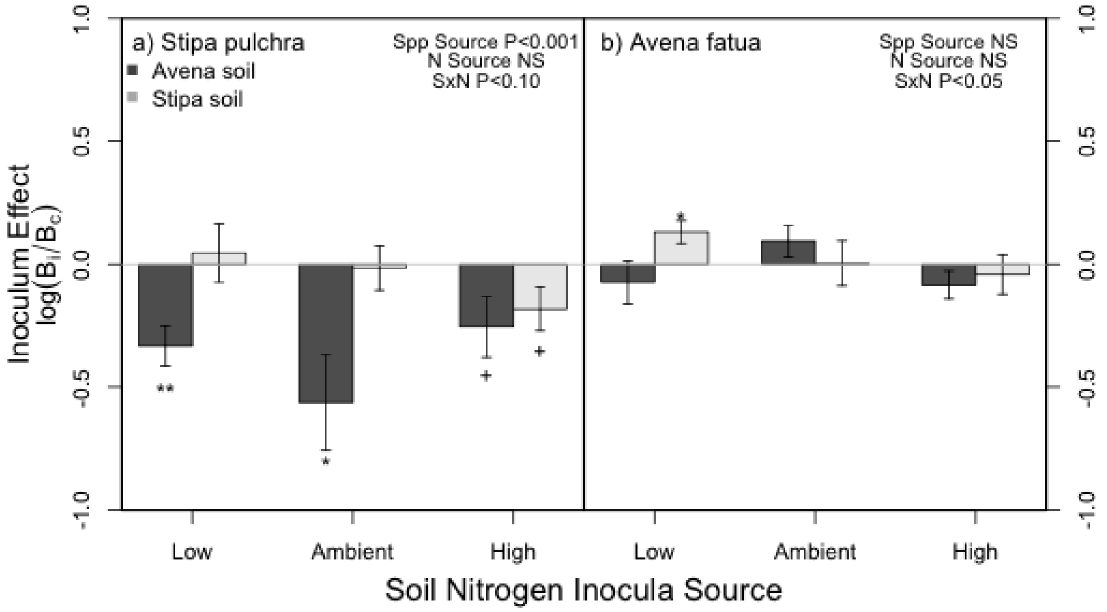


Figure 2. Effect of inoculating soil on plant performance for *Stipa pulchra* (a) and *Avena fatua* (b). *Stipa* experienced negative effects (i.e. grew worse in the inoculated soil treatments compared to sterile) when grown in heterospecific (*Avena*) soil inoculum. Soil inocula affected *Avena* growth only when grown with inoculum from the heterospecific (*Stipa)* grown under carbon addition (+C). Mean ± 1SE. Significantly different from zero: + $P<0.07$, * $P<0.05$, ** $P<0.01$

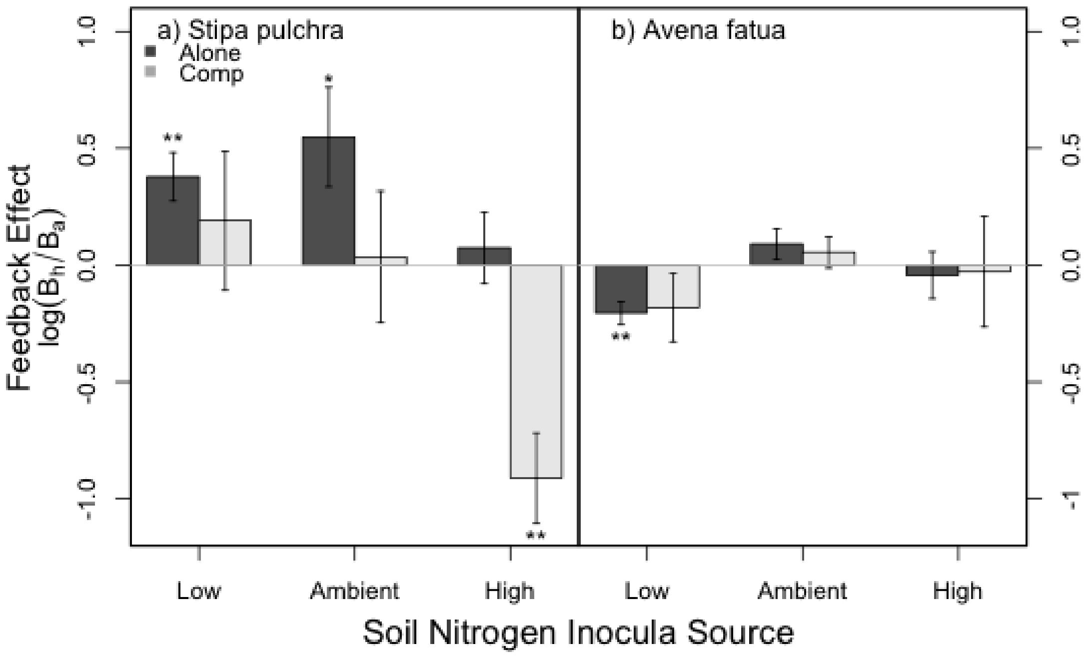


Figure 3. Plant-soil feedbacks for *Stipa pulchra* (a) and *Avena fatua* (b) grown alone or with a competitor, across soils cultured by conspecifics or heterospecifics that were grown under varying resources. *Stipa* experienced positive feedbacks (i.e. grew better with its home soil communities) when grown alone in low N and ambient N soil communities, but these feedbacks became negative when grown in high N soil communities. *Avena* grew worse in its conspecific soil compared to heterospecific low N soil communities came from low N, resulting in a negative feedback. Means ± 1SE. Significantly different from zero: * $P<0.05$, ** $P<0.01$

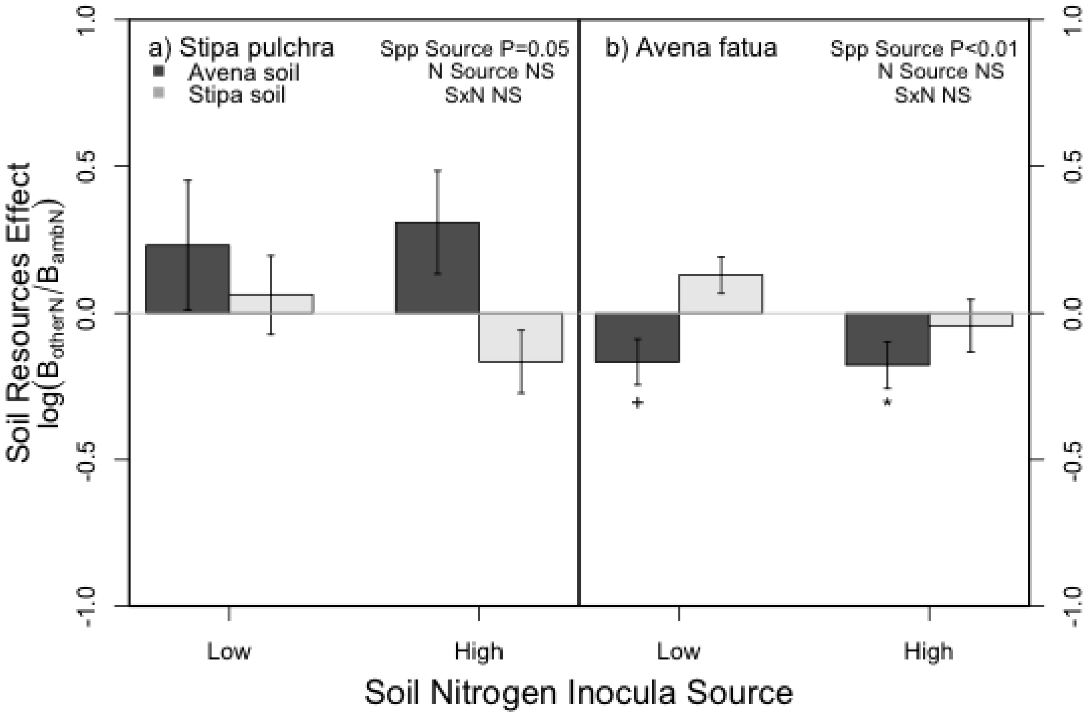


Figure 4. Effect of changes in soil community due to changes in soil nitrogen (N) resources on *Stipa pulchra* (a) and *Avena fatua* (b) growth. *Stipa* grew better in soil communities from ambient N availability compared to low or high N availability when these soils were also cultured by heterospecific, *Avena.* Conversely, *Avena* grew better in soil communities from ambient N availability when these soils were from cultured by conspecifics. Means ± 1 SE. Significantly different from zero: + P<0.07, * P<0.05

Chapter 6

The effect of seed addition, soil amendments, and neighborhood on native recovery after an extreme disturbance

Introduction

Invasion by exotic plant species has been shown to impact native diversity and function of many native ecosystems (D'Antonio and Vitousek 1992, Vila et al. 2011). For instance, in many grasslands, invasion of annual exotic grasses has altered fire frequency and nutrient cycling, and reduced species diversity (Whisenant 1990, Bobbink 1991, Vinton and Goergen 2006). While protection of the remaining native grasslands and the restoration of invaded areas are widespread management goals (Sheley et al. 2010), these goals have proven challenging, in part due to the changes in the disturbance regime and resource availability (James et al. 2013).

Disturbances can add complexity to management efforts as they can often trigger invasion by opening an “invasion window” when the native system is most vulnerable- during post-disturbance recovery (Buckley et al. 2007). For native grassland species, recovery often includes the need to recruit from seed, a stage sensitive to competitive exclusion from exotic annuals (Yu and Wilson 2001, Larios et al. *In press*). Here, I ask whether changes in competitive neighborhood and soil resource availability can increase native recruitment following a disturbance, constraining the invasion window.

Removal of exotic species prior to seed set is a common management technique aimed at reducing exotic propagules, and slowing the development of the litter thatch that may impede establishment (Bartolome 1979, Meyer and Schiffman 1999, Weiss 1999). While removal of exotic seed following a disturbance may slow the growth of the exotic populations (Tognetti and Chaneton 2012), the question remains whether it also enhances the recruitment of natives into these areas.

The invasion window could also be reduced by dampening pulses in soil nitrogen (N) availability that can follow disturbances (Radford 2013). Because many exotic species are thought to be able to capitalize on increases in N (Vitousek et al. 1997a, Brooks 2003), amendments that reduce resource availability may be able to slow invasion and allow native species that can better tolerate low resource levels a chance to establish (Alpert and Maron 2000, Blumenthal et al. 2003). Carbon (C) additions in the form of sawdust or sugar have been advocated as a technique to reduce plant available N and shift interactions in favor of native recruitment (Blumenthal et al. 2003, Cleland et al. 2012). However, as carbon amendments reduce N available to all plants, it may slow the growth of both exotic and native species (Corbin and D'Antonio 2004a, Sandel and Corbin 2010, James et al. 2011a), again bringing to question whether it enhances the recruitment of natives. An alternative approach could be to combine exotic removals with increased N, potentially reducing the negative effects of exotic competitors but providing the natives with resources to improve growth.

Here I investigate an invasion triggered by a large-scale disturbance (an intense fire following a record drought), and whether changes in competitive neighborhood (exotic species removal) and resource availability (soil amendment addition) can facilitate the reestablishment of native species. I test the assumption that both changes should improve native recruitment. In addition, I investigate whether native recruitment might be optimized at high, rather than low, levels of soil nitrogen if interactions with exotics are reduced.

Methods

Study Site

This study was conducted at Loma Ridge in Irvine, California within the Irvine Ranch Land Reserve (N:33.7501 W:-117.71787). It is characterized by a Mediterranean climate with a growing season from November to June as determined by rainfall (e.g., the 2010 growing season was from November 2009 to June 2010). The average growing season rainfall for the site was 330m from 1991-2010 with an average growing season temperature over the same period of 20.9°C. Annual precipitation over the course of the study (2009-2011) was 214, 175 and 449.3 mm, respectively (California Irrigation Management Information Services, http://wwwcimis.water.ca.gov/cimis/welcome.jsp). Loma Ridge consists of a string of grassland vegetation on the ridge top and on north and west facing slopes, a steep erosional cliff on the southern edge, and coastal sage scrub vegetation to the north on south facing slopes. The cliff and coastal sage scrub delimited most of the grassland area, which while variable was less than 0.3km in width along the ridge.

The study site burned in the 2007 arson-caused Santiago wildfire, which occurred from Oct 21 –Nov 4, 2007. This fire, which occurred after one of the driest years on record (Keeley et al. 2009), burned intensely and completely removed all aboveground vegetation and litter from the study site. In total, it burned 28,517 acres, leaving no unburned intact grassland communities within 5km (OCFA 2008).

Experimental Design

In June 2008, at the end of the first complete growing season after the fire, I identified 5 blocks, each consisting of grassland patch dominated (>50% abundance) by a native species, *Stipa pulchra* Hitchc., adjacent to a grassland patch dominated by the annual exotic, *Avena fatua* L. (nomenclature follows Baldwin et al. 2012). Within each block, I set up six 0.5 x 0.5 m plots, three within the native neighborhood patch and three within the exotic patch type. In the native plots, I removed all exotic grasses in May of the 2009 and 2010 growing seasons by clipping in the native plots; removal was aimed at reducing seed input and litter build up for the subsequent year. To best describe the invasion that occurred each year, we took response measures (see below) prior to conducting removals. We did not remove native grass biomass in the exotic patch plots, as native grasses did not naturally colonize these plots.

In each neighborhood type, I manipulated soil N availability: 1) decreased N via C addition, 2) ambient N, 3) increased N via N additions. I increased N at a rate of 6 g $N/m^2/yr^1$, which I applied in the form of calcium nitrate. I decreased soil N using table sugar at a rate of 421 g $C/m^2/yr^1$. In similar sites, this level of carbon addition decreased N by about 30% (Cleland et al. 2012). Soil amendments were applied three times over each growing season, beginning in the 2009 growing season until the end of the 2011 growing season. In total, the experiment consisted of 30 plots (5 replicate blocks x 2 patch types x 3 soil N).

Each plot was subdivided into 4 quadrants, two of which were randomly assigned to a seeding treatment: 1) native forb mix or 2) native *Stipa* perennial bunchgrass. The native forb mix consisted of six species: *Dichelostemma capitatum, Sisyrinchium bellum, Lupinus bicolor, Lupinus succulentus, Calindrinia ciliata,* and *Amsinckia menziesii.* I measured out a standard weight for each native forb that was representative of adding 100 seeds. The seeds were scattered over the assigned quadrant. For the native *Stipa* treatment we hand planted 2 seeds at each intersection of 5x5 grid, which I had marked with a blue paperclip, for a total of 50 seeds. All seeds were added by the first week of November 2009 for the 2010 growing season. Due to poor *Stipa* germination, I supplemented this seeding with five seedling transplants that I planted in mid-January. The transplanted seedlings were sown in polystyrene flats starting December 2010, and were grown outdoors prior to planting in the field.

For the annual native species I added, I measured establishment and estimated fitness by counting the amount of seeds produced (May 2010) and calculating its population growth rate (i.e., the number of seeds produced/the number of seeds added). For the perennial species (*Stipa*), I surveyed first year (growing season) survivorship (May 2010), summer (dry season) survivorship (January 2011), and second year (final) survivorship (May 2011).

To characterize the effects of my manipulations on aboveground biomass and species composition during the 2010 growing season, I also harvested all biomass within a 10x15cm subsample in one of the no seed addition quadrants. All live biomass was sorted into 5 functional groups: 1) exotic annual grasses, 2) native perennial grasses, 3) native forbs, 4) exotic forbs, and 5) litter, and then dried to a constant weight at 60$^{\circ C}$ for 48hrs. I additionally took soil samples (2, 15cm cores) within each plot, to assess gravimetric soil moisture in March 2010.

To estimate how the competitive environment affected growth of the *Stipa* seedlings, I sampled neighbor biomass around the surviving seedlings in May 2011. I divided the quadrant into a grid with 5x5cm squares and harvested all the biomass within three types of neighborhoods: 1) the 5x5cm square that contained the seedling (which I term immediate neighborhood), 2) the 5x5cm squares adjacent to the square with the seedling (inner neighborhood), and 3) the surrounding set of squares adjacent to those sampled for 2 (outer neighborhood), for a total of a 25x25cm area sampled for each seedling. I did not remove exotic biomass in 2011, as it was the last year of the experiment, and so these measurements include exotic neighbors that colonized native patches during that year.

Analyses

I analyzed establishment (survival to the end of the first growing season) of the native forbs and *Stipa* with the proc mixed procedure in SAS (version 9.1). I specified a model with neighborhood (native with exotics removed, exotics) and soil amendment (C addition, control, N addition) as fixed factors and block as a random factor. Due to the lack of establishment of the forb species, we were only able to analyze data for *Lupinus succulentus*. Population growth for *Lupinus,* and *Stipa* summer and second year survivorship, were also analyzed using the model described above. First year *Lupinus* and *Stipa* establishment were square root transformed to meet assumptions of normality, while second year *Stipa* survivorship was arc-sine transformed. I additionally corrected for heterogeneous variances within the treatments, as needed.

I assessed the effect of the competitive environment on second year biomass of the perennial *Stipa* with an ANCOVA model. *Stipa* seedling biomass at the end of the second year was the response variable, and neighborhood and soil amendments were included as categorical variables, while the neighboring 2011 exotic annual grass biomass was included as a continuous variable. Block was specified as a random effect, and I corrected for the heterogeneous variances within the removal and soil amendment interaction term. *Stipa* biomass was log transformed to meet assumptions of normality. I ran the above model varying the exotic annual biomass at the three spatial scales to assess if the competitive effects of the neighbors are scale dependent. Additionally, to tease apart whether a *Stipa* response was due to changes in neighborhood biomass or composition, I ran a mixed model with total biomass in the 25x25cm neighborhood and the relative abundance of the exotic annual grass biomass within that area as continuous fixed factors and block as a random factor.

Results

Aboveground biomass did not vary across neighborhood type (i.e. "native with exotics removed" or "exotics") and soil N treatments (neighborhood: $F_{1,20}$=0.79, P=0.39; soil N: $F_{2,20}$=1.33, P=0.29; Figure 1a). As expected, exotic annual grasses dominated the exotic annual neighborhood type (>60%, $F_{1,20}$=8.28, P<0.01), and naturally-occurring native grasses were present only in the native neighborhood type (Figure 1b). While I removed exotic grasses in the native plots at the end of each season, new invasion each year was substantial, with the native patches often containing over 50% exotic grass (Figure 1b). As expected, removal of exotic species did reduce litter mass ($F_{1,20}$=17.42, P<0.001); particularly in the control (ambient N) plots (removal x soil N interaction: $F_{2,20}$=3.87, P<0.05). However my manipulation also decreased gravimetric soil moisture within the native plots compared to the exotic (0.18 vs 0.25, respectively; neighborhood: $F_{1,17.4}$=38.4, P<0.001).

Carbon addition decreased exotic cover (soil N: $F_{2,20}$=5.35, P<0.02). C addition affected exotic cover most strongly in native patch types (neighborhood x soil N interaction, $F_{2,20}$=7.23, P<0.01; Figure 1b, solid bars), resulting in an increase in the relative abundance of native grasses. Carbon addition plots also had greater soil moisture before going into the summer months (neighborhood x soil N interaction: $F_{2,17.8}$=4.16, P<0.05). The addition of nitrogen did not affect exotic cover in either patch type.

Neighborhood type and soil amendments did not significantly affect the number of *Lupinus* individuals able to establish; however, surprisingly, establishment tended to be greater in the exotic neighborhood (neighborhood: $F_{1,20}$=3.33, P=0.08; soil N: $F_{2,20}$=0.11, P=0.89, Figure 2a). The trend for establishment strengthened in terms of population growth rate, where *Lupinus* populations grew faster in exotic, compared to native, neighborhoods (7.49 vs 1.41, $F_{1,20}$=7.55, P=0.01). This effect was particularly strong when C was added to reduce N availability in the exotic-dominated patches (neighborhood x soil N interaction, $F_{2,20}$=3.83, P<0.05, Figure 1b).

Overall, *Stipa* survivorship was less than 10% over the two years. Similar to the establishment of *Lupinus*, the number of *Stipa* individuals surviving to the end of the first growing season was not significantly affected by neighborhood or soil N amendments (neighborhood: $F_{1,20}$=0.01, P=0.93, soil N: $F_{2,20}$=2.69, P<0.10). First-year survivorship in exotic neighborhoods depended slightly on soil amendment, were C addition tended to increase and N addition tended to decrease survivorship in exotic neighborhoods (neighborhood x soil N interaction, $F_{2,20}$=3.11, P=0.07, Figure 3a). Over the summer, exotic annual neighbors enhanced *Stipa* survivorship compared to native neighborhoods with exotics removed (0.49 vs 0.31, $F_{1,19}$=4.80, P=0.04, Figure 3b), and this effect was particularly strong when C was added (pairwise contrast for neighborhood x soil N interaction: $F_{1,19}$=6.86, P<0.02; Figure 2b). The positive effect of C addition in exotic, but not native neighborhoods, persisted for *Stipa* survivorship over the entire two years (neighborhood x soil N interaction: $F_{2,20}$=3.55, P=0.05; Figure 3c).

In addition to increased survivorship, *Stipa* individuals were larger in the exotic annual neighborhood (neighborhoood: $F_{1,13}$=6.32, P=0.03; soil N:$F_{2,13}$=0.20, P=0.82). *Stipa* seedling biomass did not vary with the surrounding exotic annual grass biomass at any scale (immediate: $F_{1,67}$=1.27, P=0.26; inner: $F_{1,67}$=0.97, P=0.33; outer: $F_{1,67}$=1.27, P=0.26) or total aboveground biomass ($F_{1,66.5}$=0.24, P=0.63). *Stipa* seedlings were larger in plots with little or no perennial grasses and high relative abundance of annual exotic grass (Cover: estimate=0.037±0.016, $F_{1,68.5}$=4.65, P<0.05).

Discussion

Land managers are pressed to deal with the increasing threat of exotic annual grass invasions into perennially dominated systems, particularly in light of ecosystem N enrichment and altered disturbance regimes (Vitousek et al. 1997a, Buckley et al. 2007). Overall I found little evidence that altering the competitive neighborhood in addition to soil amendments improved native recruitment. While removing the exotic annual biomass within the native plots did reduce the litter layer, I found little evidence that removing the exotic annual biomass helped the recruitment or fitness of native forbs or perennial grass after an extreme disturbance. I found that soil amendments, specifically carbon addition, improved the fitness of the annual native forb*, Lupinus succulentus*. Surprisingly, the exotic annuals under carbon addition facilitated both the summer survivorship and final recruitment of the native perennial grass *Stipa pulchra* (Figure 3b, c; respectively). Overall, I had very low recruitment across my experiment, suggesting that within this system recruitment is constrained by factors other than species interactions or soil N resources.

Disturbances can reset recruitment dynamics and alter the relative importance of seed and establishment limitation in species recruitment (Grubb 1977, Burke and Grime 1996, Turnbull et al. 2000). An intense large disturbance can greatly reduce the seedbank, resulting in greater seed limitation (Leck et al. 1989). In this study I attempted to improve recruitment by overcoming seed limitation with my seed addition. While it is possible that for some of the smaller seeded species, I did not add sufficient seeds to overcome seed limitation, recruitment functions of annual forbs within California can shift in the presence of a competitive dominant, reducing the number of recruits even at similar seeding densities (Aicher et al. 2011). However, the positive growth rates of *Lupinus* support previous studies where seed addition has been shown to establish small persisting populations of native forbs, even in the presence of high density of exotic grasses (Seabloom et al. 2003a).

My small scale exotic annual grass removal within the native patches was aimed at minimizing the barrier that litter layers can form for recruitment (Bartolome 1979) and reducing seed inputs of the exotics (Tognetti and Chaneton 2012). However this manipulation also decreased gravimetric soil moisture within the native plots compared to the exotic, likely compromising the summer survival and subsequent growth of *Stipa* seedlings. As I observed here, soil nutrient reduction via sucrose can reduce the cover of exotic annual grasses (Blumenthal et al. 2003, Cleland et al. 2012). However, it did not minimize the competitive effect of the neighborhood on the growth of the *Stipa* seedlings, as the total biomass in the native plot did not change, suggesting that it may have increased competitive interactions with the resident natives within the plot. The usefulness of soil amendments as a restoration tool is contingent on it also facilitating the establishment and recovery of native species, and while I observed that *Lupinus* had a greater growth rate and that overall recruitment after two years was greater for *Stipa* with carbon addition, the lack of a strong overall trend suggests that other management techniques in tandem with seed additions should be considered to improve recruitment.

These results reiterate the importance of assessing a species at multiple life stages to assess effectively management efforts (James et al. 2011b, James 2012). The similar establishment of the annual forb, *Lupinus*, across the experiment suggests that my treatments did not address its specific recruitment constraints; however by additionally measuring *Lupinus'* fitness, I was able to detect that soil amendments can impact its population's seed production. For perennial plants within a Mediterranean climate, surviving the summer drought is an additional critical recruitment filter. We observed that *Stipa* summer survivorship and overall recruitment tended to be greater in the exotic annual, carbon addition plots. We also observed that the exotic annual carbon plots tended to have greater soil moisture before going into the summer months, which may have allowed *Stipa* to remain active longer in the season, increasing its summer survivorship (similar to what I observed in Chapter 2). An additional management action could be mid to late season watering to help native perennial seedlings establish and survive the summer drought as exotic annual grasses tend to deplete soil water earlier in the growing season (Holmes and Rice 1996, Kulmatiski et al. 2006).

Even though these treatments were done on a small scale, they revealed that in tandem carbon addition and removal of the exotic annual did not promote the establishment of natives in areas that were once dominated by native species. Carbon addition was able to promote the recruitment of some native species, but further management efforts should incorporate other actions that can improve the establishment of other species, such as pre-treating seeds or supplemental watering. Moreover, these results emphasize the importance of applying management actions that take into account multiple recruitment constraints and demographic processes for the successful recovery of native species (Suding et al. 2004).

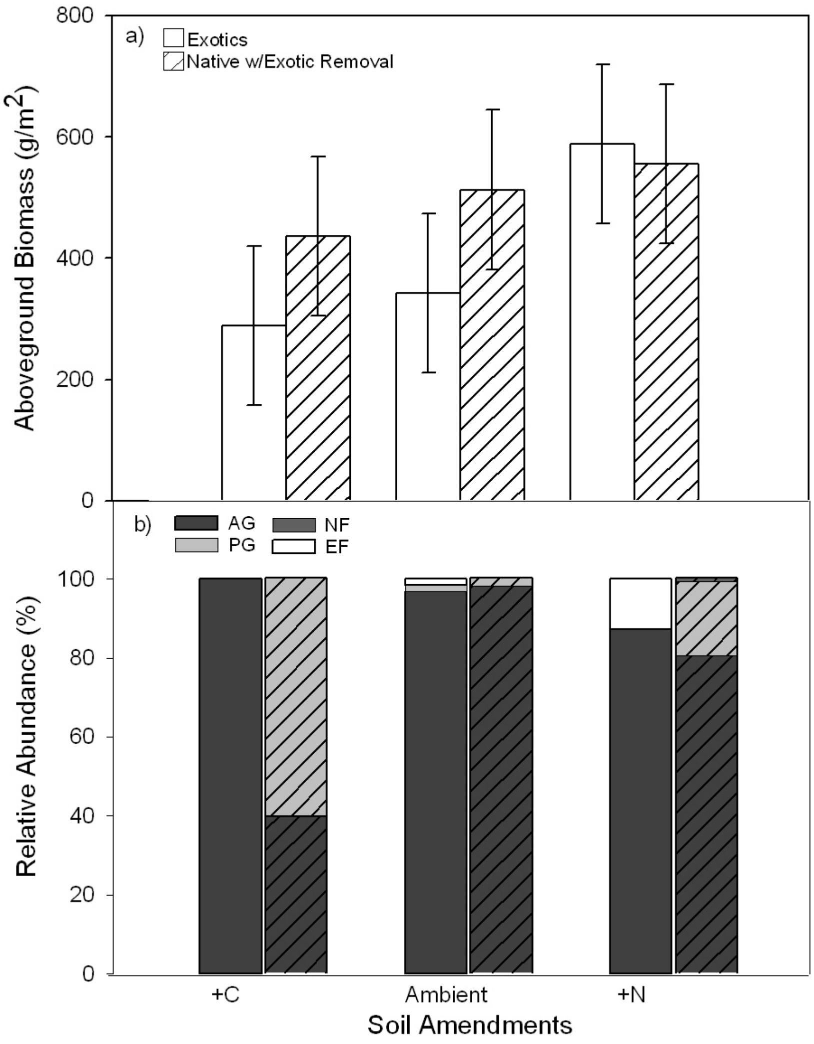


Figure 1. Aboveground biomass (a) and community composition (b) within the no seed addition plots across the neighborhood and soil N amendment treatments. Aboveground productivity (LS means ± 1SE) did not vary across the treatments. Exotic annual grass cover only varied between the neighborhood treatments under +C. AG-exotic annual grass, PG-native perennial grass, NF-native forbs, EF-exotic forbs.

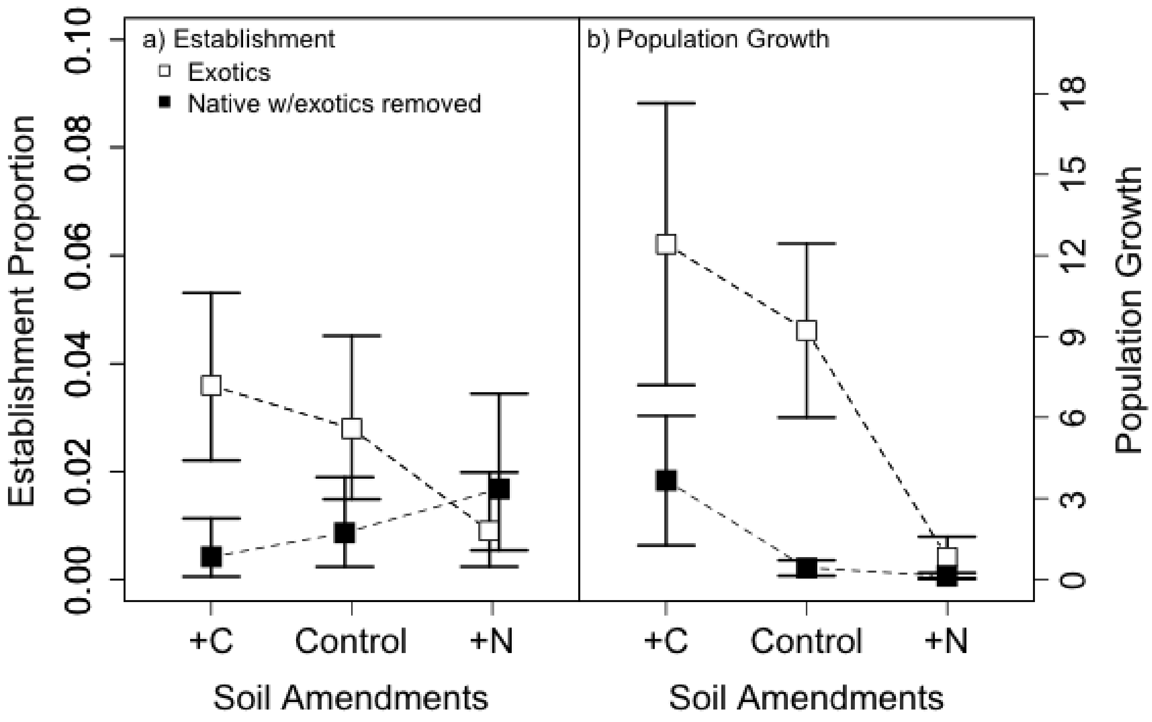


Figure 2. Establishment (a) and population growth (b) of *Lupinus succulentus* along soil nitrogen (N) amendments and neighborhood type. *Lupinus* establishment did not differ across the soil amendments or the neighborhood treatments. Population growth (b) was greater in annual exotic plots compared to native plots where the exotics were removed and lowest at high N, regardless of neighborhood. LS Means ± 1 SE. Establishment is square root back transformed.

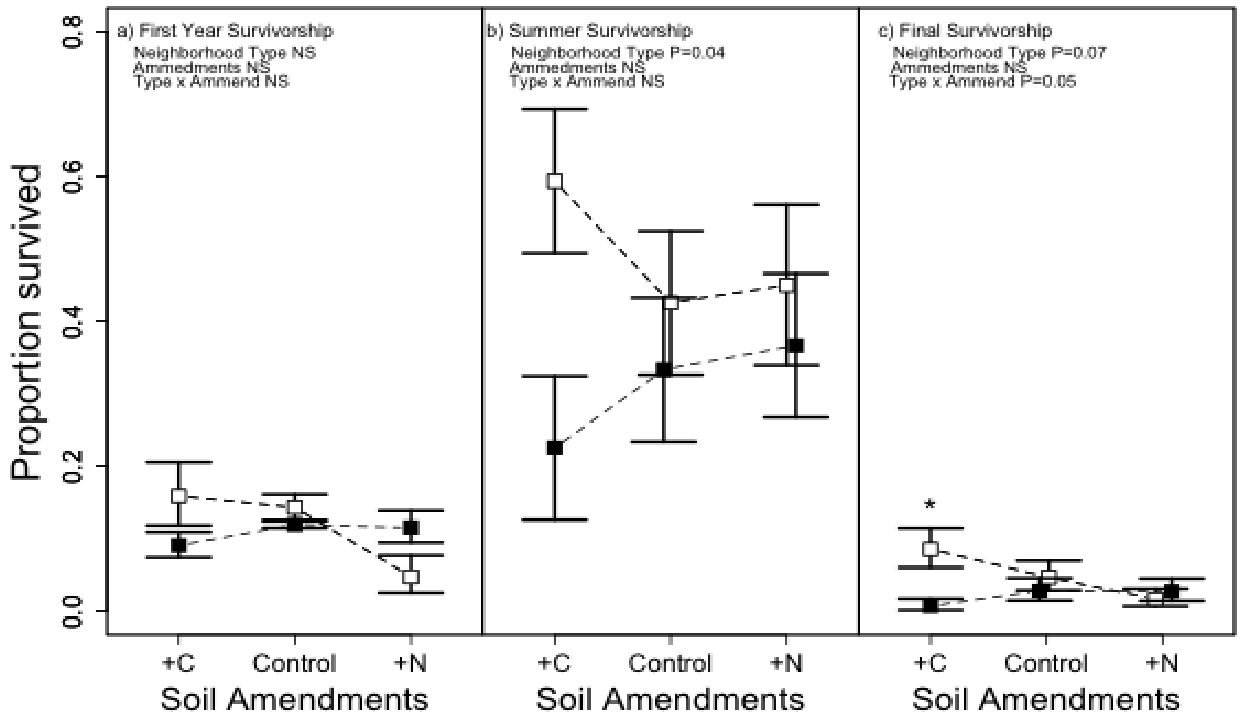


Figure 3. Survivorship of *Stipa* seedlings over the experiment. First year survivorship was low regardless of the presence of exotic annuals or soil N amendment (a). The presence of exotic annuals increased summer survivorship (b). Final survivorship after two growing seasons was greatest in plots with C addition and the presence of exotic annuals (c). LS Means ± 1 SE. First year and final survivorship are square root back transformed. Significant posthoc pair-wise differences at $P<0.05$ are indicated by *.

Literature Cited

Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. Plant Ecology **201**:445-456.

Adler, P. B., H. J. Dalgleish, and S. P. Ellner. 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? Journal of Ecology **100**:478-487.

Adler, P. B. and J. M. Drake. 2008. Environmental Variation, Stochastic Extinction, and Competitive Coexistence. American Naturalist **172**:E186-E195.

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters **10**:95-104.

Aicher, R. J., L. Larios, and K. N. Suding. 2011. Seed Supply, Recruitment, and Assembly: Quantifying Relative Seed and Establishment Limitation in a Plant Community Context. American Naturalist **178**:464-477.

Aldrich-Wolfe, L. 2007. Distinct mycorrhizal communities on new and established hosts in a transitional tropical plant community. Ecology **88**:559-566.

Allison, V. J. 2002. Nutrients, arbuscular mycorrhizas and competition interact to influence seed production and germination success in Achillea millefolium. Functional Ecology **16**:742-749.

Alpert, P. and J. L. Maron. 2000. Carbon Addition as a Countermeasure Against Biological Invasion by Plants. Biological Invasions **2**:33-40.

Bais, H. P., R. Vepachedu, S. Gilroy, R. M. Callaway, and J. M. Vivanco. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. SCIENCE **301**:1377-1380.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147-172 *in* H. G. Baker and G. L. Stebbins, editors. The Genetics of Colonizing Species. Academic Press, London, UK.

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, editors. 2012. The Jepson Manual: vascular plants of California. second edition. University of California Press, Berkeley, CA.

Bard, E. C., R. L. Sheley, J. S. Jacobsen, and J. J. Borkowski. 2004. Using ecological theory to guide the implementation of augmentative restoration. Weed Technology **18**:1246-1249.

Bardgett, R. D. and R. Cook. 1998. Functional aspects of soil animal diversity in agricultural grasslands. Applied Soil Ecology **10**:263-276.

Bardgett, R. D., J.L. Mawdsely, S. Edwards, P.J. Hobbs, J.S. Rodwell, and W.J. Davies. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. Funtional Ecology **13**:650-660.

Bardgett, R. D. and A. Shine. 1999. Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. Soil Biology and Biochemistry **31**:317-321.

Bardgett, R. D., T.C. Streeter, L.Cole, and I.R. Hartley. 2002. Linkages between soil biota, nitrogen availability, and plant nitrogen uptake in a mountain ecosystem in the Scottish Highlands. Applied Soil Ecology **19**:121-134.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. Journal of Ecology **67**:273-281.

Bartolome, J. W. and B. Gemmill. 1981. The ecological status of Stipa pulchra (poaceae) in California. Madrono **28**:172-184.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes.

Bell, J. L., L. C. Sloan, and M. A. Snyder. 2004. Regional changes in extreme climatic events: A future climate scenario. Journal of Climate **17**:81-87.

Bever, J. D. 1994. Feedback between plants and their soil communities in an old field community. Ecology **75**:1965-1977.

Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. Rooting theories of plant community ecology in microbial interactions. Trends in Ecology & Evolution **25**:468-478.

Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology **85**:561-573.

Bhagwat, S. A., E. Breman, T. Thekaekara, T. F. Thornton, and K. J. Willis. 2012. A Battle Lost? Report on Two Centuries of Invasion and Management of Lantana camara L. in Australia, India and South Africa. Plos One **7**.

Bhatt, Y. D., Y. S. Rawat, and S. P. Singh. 1994. Changes in ecosystem functioning after replacement of forest by Lantana shrubland in Kumaun Himalaya. Journal of Vegetation Science **5**:67-70.

Bissett, A., M. V. Brown, S. D. Siciliano, and P. H. Thrall. 2013. Microbial community responses to anthropogenically induced environmental change: towards a systems approach. Ecology Letters **16**:128-139.

Blanchard, R. and P. M. Holmes. 2008. Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. South African Journal of Botany **74**:421-431.

Bleier, J. S. and R. D. Jackson. 2007. Manipulating the quantity, quality, and manner of C addition to reduce soil inorganic N and increase C4 : C3 grass biomass. Restoration Ecology **15**:688-695.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. Ecological Applications **13**:605-615.

Bobbink, R. 1991. Effects of Nutrient Enrichment in Dutch Chalk Grassland. Journal of Applied Ecology **28**:28-41.

Bowler, P. A. 2008. Artichoke thistle as an ecological resource and its utility as a precursor to restoration (California). Ecological Restoration **26**:7-8.

Bradford, M. A., S. A. Wood, F. T. Maestre, J. F. Reynolds, and R. J. Warren. 2012. Contingency in ecosystem but not plant community response to multiple global change factors. New Phytologist **196**:462-471.

Bradley, K., R. A. Drijber, and J. Knops. 2006. Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi. Soil Biology & Biochemistry **38**:1583-1595.

Brandt, A. J. and E. W. Seabloom. 2012. Seed and establishment limitation contribute to long-term native forb declines in California grasslands. Ecology **93**:1451-1462.

Brandt, A. J., E. W. Seabloom, and P. R. Hosseini. 2009. Phylogeny and provenance affect plant-soil feedbacks in invaded California grasslands. Ecology **90**:1063-1072.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin Ecological Monographs **27**:326-349.

Briske, D. D., S. D. Fuhlendor, and E. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. Rangeland Ecology & Management **58**:1-10.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology **40**:344-353.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution **18**:119-125.

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Buisson, E., S. Anderson, K. D. Holl, E. Corcket, G. F. Hayes, A. Peeters, and T. Dutoit. 2008. Reintroduction of Nassella pulchra to California coastal grasslands: Effects of topsoil removal, plant neighbour removal and grazing. Applied Vegetation Science **11**:195-204.

Burke, M. J. W. and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Callaway, R., D. Cipollini, K. Barto, G. C. Thelen, S. G. Hallett, D. Prati, K. A. Stinson, and J. Klironomos. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology **89**:1043-1055.

Callaway, R. M. and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment **2**:436-443.

Callaway, R. M., G. C. Thelen, S. Barth, P. W. Ramsey, and J. E. Gannon. 2004. Soil fungi alter interactions between the invader Centaurea maculosa and North American natives. Ecology **85**:1062-1071.

Chapman, S. K., J.A. Langley, S.C. Hart, and G.W. Koch. 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. New Phytologist **169**:27-34.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia **136**:489-498.

Chase, J. M. and M. A. Leibold. 2003. Ecological Niches: Linking classical and contemporary approaches. University of Chicago Press, Chicago.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Cione, N. K., P. E. Padgett, and E. B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. Restoration Ecology **10**:376-384.

Clark, B. R., S. E. Hartley, K. N. Suding, and C. de Mazancourt. 2005. The effect of recycling on plant competitive hierarchies. American Naturalist **165**:609-622.

Cleland, E. E., C. M. Clark, S. L. Collins, J. E. Fargione, L. Gough, K. L. Gross, S. C. Pennings, and K. N. Suding. 2011. Patterns of trait convergence and divergence among native and exotic species in herbaceous plant communities are not modified by nitrogen enrichment. Journal of Ecology **99**:1327-1338.

Cleland, E. E., L. Larios, and K. N. Suding. 2012. Strengthening invasion filters to re-assemble native plant communities: soil resources and phenological overlap. Restoration Ecology.

Clements, F. E. 1916. Plant succession. Carnegie Institution Washington.

Clewell, A. and T. McDonald. 2009. Relevance of Natural Recovery to Ecological Restoration. Ecological Restoration **27**:122-124.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions **8**:1023-1037.

Coleman, H. M. and J. M. Levine. 2007. Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. Biological Invasions **9**:65-71.

Collins, S. L. 1990. Patterns of community structure during succession in tall grass prairie. Bulletin of the Torrey Botanical Club **117**:397-408.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science:1302-1310.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization American Naturalist **111**:1119-1144.

Conser, C. and E. F. Connor. 2009. Assessing the residual effects of Carpobrotus edulis invasion, implications for restoration. Biological Invasions **11**:349-358.

Cook, W. M., J. Yao, B. L. Foster, R. D. Holt, and L. B. Patrick. 2005. Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. Ecology **86**:1267-1279.

Corbin, J. D. and C. M. D'Antonio. 2004a. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology **12**:36-43.

Corbin, J. D. and C. M. D'Antonio. 2004b. Competition between native perennial and exotic annual grasses: Implications for an historical invasion. Ecology **85**:1273-1283.

Corbin, J. D. and C. M. D'Antonio. 2004c. Effects of exotic species on soil nitrogen cycling: Implications for restoration. Weed Technology **18**:1464-1467.

Cowles, H. C. 1899. The ecological relations of the vegetation ont he sand dunes of Lake Michigan. Botanical Gazette **27**:95-117.

Cox, R. D. and E. B. Allen. 2008. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. Plant Ecology **198**:37-46.

Crawley, M. J. 1987. What makes a community invasible? Pages 429-453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, Succession and Stability. Blackwell Scientific, Oxford.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters **2**:140-148.

Cushman, J. H., C. J. Lortie, and C. E. Christian. 2011. Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. Journal of Ecology **99**:524-531.

D'Antonio, C., T. L. Dudley, and M. C. Mack. 1999. Disturbance and biological invasions: direct effects and feedbacks. Pages 413-452 *in* L. R. Walker, editor. Ecosystems of Disturbed Ground. Elsevier, New York.

D'Antonio, C., J. M. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: A California perspective. Journal of Mediterranean Ecology **2**:233-245.

D'Antonio, C. and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: A synthesis. Restoration Ecology **10**:703-713.

D'Antonio, C. M. and J. C. Chambers. 2006. Using Ecological Theory to Manage or Restore Ecosystems Affected by Invasive Plant Species. Pages 260-279 *in* D. A. Falk, M. A. Palmer, and J. B. Zedler, editors. Foundations of Restoration Ecology. Island Press, Washington, DC.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological Invasions by Exotic Grasses, the Grass Fire Cycle, and Global Change. Annual Review of Ecology and Systematics **23**:63-87.

Davies, K. W., T. J. Svejcar, and J. D. Bates. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. Ecological Applications **19**:1536-1545.

del Moral, R., L. R. Walker, and J. P. Bakker. 2007. Insights Gained from Succession for the restoration of Landscpae Structure and Function. Pages 19-44 *in* L. R. Walker, J. Walker, and R. J. Hobbs, editors. Linking Restoration and Ecological Succession. Springer, New York, NY.

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science **9**:113-122.

Diaz, S., M. Cabido, and F. Casanoves. 1999. Functional implications of trait-environment linkages in plant communities.*in* E. Weiher and P. A. Keddy, editors. Ecological Assembly Rules. Cambridge University Press, Cambridge, UK.

Dickson, T. L. and B. L. Foster. 2011. Fertilization decreases plant diversity even when light is not limiting. Ecology Letters **14**:380-388.

Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution **22**:489-496.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends in Ecology & Evolution **20**:470-474.

Diez, J. M., H. L. Buckley, B. S. Case, M. A. Harsch, A. R. Sciligo, S. R. Wangen, and R. P. Duncan. 2009. Interacting effects of management and environmental variability at multiple scales on invasive species distributions. Journal of Applied Ecology **46**:1210-1218.

Diez, J. M., C. M. D'Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. B. Sorte, D. M. Blumenthal, B. A. Bradley, R. Early, I. Ibanez, S. J. Jones, J. J. Lawler, and L. P. Miller. 2012. Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment **10**:249-257.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (Centaurea solstitialis) and enhanced native plant diversity. Weed Science **47**:233-242.

DiVittorio, C. T., J. D. Corbin, and C. M. D'Antonio. 2007. Spatial and temporal patterns of seed dispersal: An important determinant of grassland invasion. Ecological Applications **17**:311-316.

Doren, R. F., J. H. Richards, and J. C. Volin. 2009a. A conceptual ecological model to facilitate understanding the role of invasive species in large-scale ecosystem restoration. Ecological Indicators **9**:S150-S160.

Doren, R. F., J. C. Volin, and J. H. Richards. 2009b. Invasive exotic plant indicators for ecosystem restoration: An example from the Everglades restoration program. Ecological Indicators **9**:S29-S36.

Doren, R. F. and L. D. Whiteaker. 1990. Efffects of fire on different size individuals of Schinus terbinthifolius. Natural Areas Journal **10**:107-113.

Dyer, A. R. 2003. Burning and grazing management in a California grassland: Growth, mortality, and recruitment of Nassella pulchra. Restoration Ecology **11**:291-296.

Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of Nassella pulchra in a California grassland. Madrono **43**:316-333.

Dyer, A. R. and K. J. Rice. 1997. Intraspecific and diffuse competition: The response of Nassella pulchra in a California grassland. Ecological Applications **7**:484-492.

Dyer, A. R. and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. Ecology **80**:2697-2710.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources **30**:75-115.

Eppinga, M. B., M. Rietkerk, S. C. Dekker, P. C. De Ruiter, and W. H. Van der Putten. 2006. Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos **114**:168-176.

Eppstein, M. J. and J. Molofsky. 2007. Invasiveness in plant communities with feedbacks. Ecology Letters **10**:253-263.

Evans, M. R., K. J. Norris, and T. G. Benton. 2012. Predictive ecology: systems approaches Introduction. Philosophical Transactions of the Royal Society B-Biological Sciences **367**:163-169.

Everitt, B. and T. Hothorn. 2011. An Introduction to Applied Multivariate Analysis with R. Springer, London.

Eviner, V. T. and C. V. Hawkes. 2008. Embracing Variability in the Application of Plant-Soil Interactions to the Restoration of Communities and Ecosystems. Restoration Ecology **16**:713-729.

Fargione, J. E. and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters **8**:604-611.

Fenn, M. E., R. Haeuber, G. S. Tonnesen, J. S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, H. M. Rueth, and J. O. Sickman. 2003. Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience **53**:391-403.

Fensham, R. J., R. J. Fairfax, and R. J. Cannell. 1994. The invasions of Lantana camara L. in Forty-Mile Scrub National Park, north Queensland Australian Journal of Ecology **19**:297-305.

Firn, J., T. Rout, H. Possingham, and Y. M. Buckley. 2008. Managing beyond the invader: manipulating disturbance of natives simplifies control efforts. Journal of Applied Ecology **45**:1143-1151.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Fox, B. J., J. E. Taylor, M. D. Fox, and C. Williams. 1997. Vegetation changes across edges of rainforest remnants. Biological Conservation **82**:1-13.

Foxcroft, L. C. and D. M. Richardson. 2003. Managing alien plant invasions in the Kruger National Park, South Africa. Pages 385-403 *in* L. E. Child, J. H. Brock, G. Brundu, K. Prach, P. Pysek, P. M. Wade, and M. Williamson, editors. Plant Invasions: Ecological Threats and Management Solutions. Backhuys Publishers, Leiden, The Netherlands.

French, K., T. J. Mason, and N. Sullivan. 2011. Recruitment limitation of native species in invaded coastal dune communities. Plant Ecology **212**:601-609.

Friedel, M. H. 1991. Range Condition Assessment and the Concept of Thresholds - a Viewpoint. Journal of Range Management **44**:422-426.

Fukami, T. and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? Ecology Letters **14**:973-984.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution **23**:695-703.

Gaertner, M., P. M. Holmes, and D. M. Richardson. 2012. Biological invasions, resilience and restoration. Pages 265-280 *in* J. van Andel and J. Aronson, editors. Restoration Ecology - The New Frontier. Wiley-Blackwell, Oxford.

Gaertner, M., D. M. Richardson, and S. D. J. Privett. 2011. Effects of Alien Plants on Ecosystem Structure and Functioning and Implications for Restoration: Insights from Three Degraded Sites in South African Fynbos. Environmental Management **48**:57-69.

Galatowitsch, S. and D. M. Richardson. 2005. Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. Biological Conservation **122**:509-521.

Gelbard, J. L. and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology **17**:420-432.

Gelbard, J. L. and S. Harrison. 2003. Roadless habitats as refuges for native grasslands: Interactions with soil, aspect, and grazing. Ecological Applications **13**:404-415.

Gentle, C. B. and J. A. Duggin. 1997. Lantana camara L. invasions in dry rainforest open forest ecotones: The role of disturbances associated with fire and cattle grazing. Australian Journal of Ecology **22**:298-306.

Gleason, H. A. 1926. The Individualistic concept of the plant association. Bulletin of the Torrey Botanical Club **53**:7-26.

Gleeson, S. K. and D. Tilman. 1994. Plant allocation, growth-rate and successional status Functional Ecology **8**:543-550.

Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen, editors. 1992. Plant Succession. Theory and Prediction. Chapman & Hall, London, UK.

Goldberg, D. E. and T. E. Miller. 1990. Effects of Different Resource Additions on Species-Diversity in an Annual Plant Community. Ecology **71**:213-225.

Gooden, B., K. French, P. J. Turner, and P. O. Downey. 2009. Impact threshold for an alien plant invader, Lantana camara L., on native plant communities. Biological Conservation **142**:2631-2641.

Greer, K. A. 2005. Habitat conservation planning in San Diego County, California: Lessons learned after five years of implementation. Environmental Practice **6**:230-239.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology **86**:902-910.

Grman, E. and K. N. Suding. 2010. Within-Year Soil Legacies Contribute to Strong Priority Effects of Exotics on Native California Grassland Communities. Restoration Ecology **18**:664-670.

Grubb, P. J. 1977. Maintenance of species richness in plant communities: importance of regeneration niches. Biological Reviews of the Cambridge Philosophical Society **52**:107-145.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia **121**:518-526.

Harpole, W. S., D. L. Potts, and K. N. Suding. 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. Global Change Biology **13**:2341-2348.

Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. Restoration Ecology **7**:376-381.

Hausmann, N. T. and C. V. Hawkes. 2009. Plant neighborhood control of arbuscular mycorrhizal community composition. New Phytologist **183**:1188-1200.

Hausmann, N. T. and C. V. Hawkes. 2010. Order of plant host establishment alters the composition of arbuscular mycorrhizal communities. Ecology **91**:2333-2343.

Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. Plant and Soil **281**:369-380.

Hawkes, C. V., I. F. Wren, D. J. Herman, and M. K. Firestone. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecology Letters **8**:976-985.

Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences of the United States of America **101**:12422-12427.

Heady, H. F. 1977. Valley Grassland. Pages 491-514 *in* M. G. a. M. Barbour, J., editor. Terrestrial Vegetation of California. J. Wiley and Sons, New York.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. Annual Review of Ecology, Evolution, and Systematics, Vol 43 **43**:227-248.

HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. California annual grass invaders: the drivers or passengers of change? Journal of Ecology **98**:1147-1156.

Hobbs, R. J. and J. A. Harris. 2001. Restoration ecology: Repairing the Earth's ecosystems in the new millennium. Restoration Ecology **9**:239-246.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion - implications for conservation. Conservation Biology **6**:324-337.

Hobbs, R. J., A. Jentsch, and V. M. Temperton. 2007. Restoration as a Process of Assembly and Succesion Mediated by Disturbance. Pages 150-167 *in* L. R. Walker, J. Walker, and R. J. Hobbs, editors. Linking Restoration and Ecological Succession. Springer, New York, NY.

Hobbs, R. J. and H. A. Mooney. 1995. Spatial and Temporal Variability in California Annual Grassland - Results from a Long-Term Study. Journal of Vegetation Science **6**:43-56.

Hobbs, R. J. and D. M. Richardson. 2011. Invasion ecology and restoration ecology: parallel evolution in two fields of endeavour. Pages 61-69 *in* D. M. Richardson, editor. Fifty Years of Invasivion Ecology: The Legacy of Charles Elton. Blackwell Publishing, West Sussex.

Hocking, M., S. Stolton, and N. Dudley. 2000. Evaluating Effectiveness: A Framework for Assessing the Mangement of Protected Areas. IUCN, Gland, Switzerland, and Cambridge, UK.

Holl, K. D. and T. M. Aide. 2011. When and where to actively restore ecosystems? Forest Ecology and Management **261**:1558-1563.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holmes, T. H. and K. J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Annals of Botany **78**:233-243.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structrure in Californian serpentine grassland Ecology **71**:478-491.

Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions **10**:167-178.

Inderjit and W. H. van der Putten. 2010. Impacts of soil microbial communities on exotic plant invasions. Trends in Ecology & Evolution **25**:512-519.

Ives, A. R. 1995. Predicting the response of populations to environmental change. Ecology **76**:926-941.

Jackson, L. E. 1985. Ecological Origins of Californias Mediterranean Grasses. Journal of Biogeography **12**:349-361.

Jackson, R. D. and J. W. Bartolome. 2002. A state-transition approach to understanding nonequilibrium plant community dynamics in Californian grasslands. Plant Ecology **162**:49-65.

James, J. J. 2012. Species Performance: the Relationship Between Nutrient Availability, Life History Traits, and Stress. Pages 142-153 *in* T. A. Monaco and R. L. Sheley, editors. Invasive Plant Ecology and Management: Linking Processes to Practice.

James, J. J., R. E. Drenovsky, T. A. Monaco, and M. J. Rinella. 2011a. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? Ecological Applications **21**:490-502.

James, J. J., R. L. Sheley, T. Erickson, K. S. Rollins, M. H. Taylor, and K. W. Dixon. 2013. A systems approach to restoring degraded drylands. Journal of Applied Ecology **50**:730-739.

James, J. J., B. S. Smith, E. A. Vasquez, and R. L. Sheley. 2010. Principles for Ecologically Based Invasive Plant Management. Invasive Plant Science and Management **3**:229-239.

James, J. J., T. J. Svejcar, and M. J. Rinella. 2011b. Demographic processes limiting seedling recruitment in arid grassland restoration. Journal of Applied Ecology **48**:961-969.

Jentsch, A. 2007. The challenge to restore processes in face of nonlinear dynamics- On the crucial role of disturbance regimes. Restoration Ecology **15**:334-339.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. Oikos **69**:373-386.

Jones, H. P. and O. J. Schmitz. 2009. Rapid Recovery of Damaged Ecosystems. Plos One **4**:6.

Kardol, P., T. M. Bezemer, and W. H. van der Putten. 2006. Temporal variation in plant-soil feedback controls succession. Ecology Letters **9**:1080-1088.

Keane, R. M. and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution **17**:164-170.

Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecological Applications **15**:2109-2125.

Keeley, J. E., J. Franklin, and C. D'Antonio. 2011. Fire and Invasive Plants on California Landscapes. Pages 193-221 *in* D. M. C. F. D. A. McKenzie, editor. Landscape Ecology of Fire.

Keeley, J. E., H. Safford, C. J. Fotheringham, J. Franklin, and M. Moritz. 2009. The 2007 Southern California Wildfires: Lessons in Complexity. Journal of Forestry **107**:287-296.

Keenleyside, K. A., N. Dudley, S. Cairns, C. M. Hall, and S. Stolton. 2012. Ecological restoration for protected areas: Principles, guidelines and best practices. IUCN, Gland, Switzerland.

Kelly, M. 2000. Cynara cardunculus. Pages 139-145 *in* C. C. Bossard, J. M. Randall, and M. C. Hoshovsky, editors. Invasive Plants of California's Wildlands. University of California Press, Berkeley.

Kettenring, K. M. and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48**:970-979.

Kindt, R. and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre, Nairobi.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature **417**:67-70.

Kotanen, P. M. 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. Canadian Journal of Botany-Revue Canadienne De Botanique **75**:352-361.

Kotanen, P. M. 2004. Revegetation following soil disturbance and invasion in a Californian meadow: a 10-year history of recovery. Biological Invasions **6**:245-254.

Kulmatiski, A. 2006. Exotic plants establish persistent communities. Plant Ecology **187**:261-275.

Kulmatiski, A., K. H. Beard, and J. M. Stark. 2006. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant and Soil **288**:271-284.

Larios, L., R. J. Aicher, and K. N. Suding. In press. Effect of propagule pressure on recovery of a California grasslands after an extreme disturbance. . Journal of Vegetation Science.

Le Maitre, D. C., M. Gaertner, E. Marchante, E. J. Ens, P. M. Holmes, A. Pauchard, P. J. O'Farrell, A. M. Rogers, R. Blanchard, J. Blignaut, and D. M. Richardson. 2011. Impacts of invasive Australian acacias: implications for management and restoration. Diversity and Distributions **17**:1015-1029.

Le Maitre, D. C., D. B. Versfeld, and R. A. Chapman. 2000. The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. Water Sa **26**:397-408.

Leck, M. A., V. T. Parker, and R. L. Simpson, editors. 1989. Ecology of soil seed banks. Academic Press, San Diego, CA.

Lekberg, Y., R. T. Koide, J. R. Rohr, L. Aldrich-Wolfe, and J. B. Morton. 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. Journal of Ecology **95**:95-105.

Lepik, M., J. Liira, and K. Zobel. 2004. The space-use strategy of plants with different growth forms, in a field experiment with manipulated nutrients and light. Folia Geobotanica **39**:113-127.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters **7**:975-989.

Levine, J. M. and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Biology **17**:322-326.

Levine, J. M. and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. Annual Review of Ecology Evolution and Systematics **34**:549-574.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:775-781.

Levins, R. and D. Culver. 1971. Regional coexistence of specis and competition between rare species Proceedings of the National Academy of Sciences of the United States of America **68**:1246-&.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution **20**:223-228.

Lockwood, J. L. and C. L. Samuels. 2004. Assembly Models and the Practice of Restoration. Pages 55-70 *in* V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Island Press, Washington, DC.

Lockwood, M., G. L. Worboys, and A. Kothari, editors. 2006. Managing Protected Areas. Earthscan, London, UK.

Lowe, S. J., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species from the Global Invasive Species Database. Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), Auckland, New Zealand.

Lulow, M. E. 2006. Invasion by non-native annual grasses: The importance of species biomass, composition, and time among California native grasses of the Central Valley. Restoration Ecology **14**:616-626.

Luque, G. M., M. E. Hochberg, M. Holyoak, M. Hossaert, F. Gaill, and F. Courchamp. 2013. Ecological effects of environmental change. Ecology Letters **16**:1-3.

MacArthur, R. and R. Levins. 1967. Limiting Similarity Convergence and Divergence of Coexisting Species. American Naturalist **101**:377-&.

Macdonald, I. A. W. 1984. Is the fynbos biome especially susceptible to invasion by alien plants - a re-analysis of available data South African Journal of Science **80**:369-377.

Macdonald, I. A. W. 2004. Recent research on alien plant invasions and their management in South Africa: A review of the inaugural research symposium of the Working for Water programme. South African Journal of Science **100**:21-26.

Macdonald, I. A. W., D. M. Graber, S. Debenedetti, R. H. Groves, and E. R. Fuentes. 1988. Introduced species in nature reserves in Mediterranean-type climatic regions of the world. Biological Conservation **44**:37-66.

Macdonald, I. A. W. and D. M. Richardson. 1986. Alien species in terrestrial ecosystems of the fynbos biome. Pages 77-91 *in* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The Ecology and Management of Biological Invasions in Southern Africa. Oxford University Press, Cape Town.

MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. Plant invasions and the niche. Journal of Ecology **97**:609-615.

MacDougall, A. S. and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology **86**:42-55.

Mack, M. C. and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Mack, M. C., C. M. D'Antonio, and R. E. Ley. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C-4 grasses in Hawaii. Ecological Applications **11**:1323-1335.

Major, J. and W. T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Plant Ecology **13**:253-282.

Malmstrom, C. M., C. C. Hughes, L. A. Newton, and C. J. Stoner. 2005. Virus infection in remnant native bunchgrasses from invaded California grasslands. New Phytologist **168**:217-230.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature **466**:752-U710.

Mangla, S., Inderjit, and R. M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. Journal of Ecology **96**:58-67.

Marushia, R. G. and J. S. Holt. 2006. The effects of habitat on dispersal patterns of an invasive thistle, Cynara cardunculus. Biological Invasions **8**:577-593.

McAfee, L. 2008. Nature Reserve of Orange County Annual Report. Nature Reserve of Orange County, Irvine, CA.

McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biological Conservation **146**:1-13.

McKinney, M. L. and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution **14**:450-453.

McNeely, J. A. 2001. Invasive species: a costly catastrophe for native biodiversity. Land Use and Water Resources Research **1**:1-10.

McNeely, J. A. 2006. As the world gets smaller, the chances of invasion grow. Euphytica **148**:5-15.

Meiners, S. J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. Ecology **88**:1098-1104.

Meiners, S. J., S. T. A. Pickett, and M. L. Cadenasso. 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography **25**:215-223.

Menke, J. W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia **20**:22-25.

Meyer, M. D. and P. M. Schiffman. 1999. Fire season and mulch reduction in a California grasslands: a comparison of restoration strategies. Madrono **46**:25-37.

Milbau, A. and I. Nijs. 2004. The role of species traits (invasiveness) and ecosystem characteristics (invasibility) in grassland invasions: A framework. Weed Technology **18**:1301-1304.

Milton, S. J. and A. V. Hall. 1981. Reproductive biology of Australian Acacias in the southwestern Cape-Province, South Africa Transactions of the Royal Society of South Africa **44**:465-485.

Moody, M. E. and R. N. Mack. 1988. Controlling the spread of plant invasions - the importance of nascent foci Journal of Applied Ecology **25**:1009-1021.

Mori, A. S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology **48**:280-292.

Murcia, C. 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. Forest Ecology and Management **99**:163-170.

Noble, I. R. and R. O. Slatyer. 1980. The Use of Vital Attributes to Predict Successional Changes in Plant-Communities Subject to Recurrent Disturbances. Vegetatio **43**:5-21.

OCFA (Orange County Fire Authority). 2008. After action report Santiago Fire. Available at http://www.ocfa.org/Content/NewsEvents/OCFAReports.aspx Accessed October 2011.

Padgett, P. E. and E. B. Allen. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology **144**:93-101.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535-545.

Pearson, J., D. M. Wells, K. J. Seller, A. Bennett, A. Soares, J. Woodall, and M. J. Ingrouille. 2000. Traffic exposure increases natural (15)N and heavy metal concentrations in mosses. New Phytologist **147**:317-326.

Perry, L. G., C. Johnson, E. R. Alford, J. M. Vivanco, and M. W. Paschke. 2005. Screening of grassland plants for restoration after spotted knapweed invasion. Restoration Ecology **13**:725-735.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. Ecosystems **10**:790-796.

Pickett, S. T. A., M. L. Cadenasso, and S. J. Meiners. 2009. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. Applied Vegetation Science **12**:9-21.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. A hierarchical consideration of causes and mechanisms of succession Vegetatio **69**:109-114.

Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hiearchical levels Oikos **54**:129-136.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. D. C. Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models. .

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. D. C. Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. .

Pitt, M. D. and H. F. Heady. 1978. Responses of Annual Vegetation to Temperature and Rainfall Patterns in Northern California. Ecology **59**:336-350.

Platt, W. J. and J. H. Connell. 2003. Natural disturbances and directional replacement of species. Ecological Monographs **73**:507-522.

Potts, D. L., W. S. Harpole, M. L. Goulden, and K. N. Suding. 2008. The impact of invasion and subsequent removal of an exotic thistle, Cynara cardunculus, on CO2 and H2O vapor exchange in a coastal California grassland. Biological Invasions **10**:1073-1084.

Prach, K., S. Bartha, C. B. Joyce, P. Pysek, R. van Diggelen, and G. Wiegleb. 2001. The role of spontaneous vegetation succession in ecosystem restoration: A perspective. Applied Vegetation Science **4**:111-114.

Prach, K. and R. J. Hobbs. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restoration Ecology **16**:363-366.

Prach, K., R. Marrs, P. Pysek, and R. van Diggelen. 2007. Manipulation of Succession. Pages 121-149 *in* L. R. Walker, J. Walker, and R. J. Hobbs, editors. Linking Restoration and Ecological Succession. Springer, New York, NY.

Prach, K. and L. R. Walker. 2011. Four opportunities for studies of ecological succession. Trends in Ecology & Evolution **26**:119-123.

Prober, S. M., I. D. Lunt, and J. W. Morgan. 2009. Rapid Internal Plant-Soil Feedbacks Lead to Alternative Stable States in Temperate Australian Grassy Woodlands. Pages 156-168 *in* R. J. Hobbs and K. N. Suding, editors. New Models for Ecosystem Dynamics and Restoration. Island Press, Washington, DC.

Radford, I. J. 2013. Fluctuating resources, disturbance and plant strategies: diverse mechanisms underlying plant invasions. Journal of Arid Land **5**:284-297.

Rajaniemi, T. K., V. J. Allison, and D. E. Goldberg. 2003. Root competition can cause a decline in diversity with increased productivity. Journal of Ecology **91**:407-416.

RDevelopmentCoreTeam. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reiner, R. J. 2007. Fire in California grasslands. Pages 207-217 *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California Grasslands Ecology and Management. University of California Press, Berkeley.

Reinhart, K. O. and R. M. Callaway. 2006. Soil biota and invasive plants. New Phytologist **170**:445-457.

Rejmanek, M. and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology **84**:2281-2291.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sandel, B. and J. D. Corbin. 2010. Scale, disturbance and productivity control the native-exotic richness relationship. Oikos **119**:1281-1290.

Seabloom, E. W. 2011. Spatial and temporal variability in propagule limitation of California native grasses. Oikos **120**:291-301.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003a. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications **13**:575-592.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003b. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384-13389.

Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and the Environment **6**:547-553.

Shah, M. A., Z. A. Reshi, and D. P. Khasa. 2009. Arbuscular Mycorrhizas: Drivers or Passengers of Alien Plant Invasion. Botanical Review **75**:397-417.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution **17**:170-176.

Sheley, R., J. James, B. Smith, and E. Vasquez. 2010. Applying Ecologically Based Invasive-Plant Management. Rangeland Ecology & Management **63**:605-613.

Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. Ecological Monographs **76**:365-379.

Siguenza, C., L. Corkidi, and E. B. Allen. 2006. Feedbacks of soil inoculum of mycorrhizal fungi altered by N deposition on the growth of a native shrub and an invasive annual grass. Plant and Soil **286**:153-165.

Sirulnik, A. G., E. B. Allen, T. Meixner, and M. F. Allen. 2007. Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. Soil Biology & Biochemistry **39**:24-32.

Sperry, L. J., J. Belnap, and R. D. Evans. 2006. Bromus tectorum invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology **87**:603-615.

Stock, D. 2004. The Dynamics of Lantana camara (L.) Invasion of Subtropical Rainforest in Southeastern Australia. Griffith University, Gold Coast Campus, Queensland.

Stock, D. 2005. Management of Lantana in eastern Australia subtropical rainforests.*in* G. L. Worboys, M. Lockwood, and T. De Lacy, editors. Protected Area Management: Principles and Practices. Oxford University Press, Melbourne.

Stromberg, M. R. and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications **6**:1189-1211.

Suding, K. N. 2011. Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. Pages 465-487 *in* D. J. Futuyma, H. B. Shaffer, and D. Simberloff, editors. Annual Review of Ecology, Evolution, and Systematics, Vol 42.

Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America **102**:4387-4392.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution **19**:46-53.

Suding, K. N., W. S. Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and W. H. van der Putten. 2013. Consequences of plant-soil feedbacks in invasion. Journal of Ecology **101**:298-308.

Suding, K. N. and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution **24**:271-279.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Diaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology **14**:1125-1140.

Swarbick, J. T. 1986. History of the lantanas in Australia and origins of the weedy biotypes. Plant Protection Quarterly **1**:115-121.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications **17**:1388-1402.

Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle, editors. 2004. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Island Press, Washington, DC.

Templer, P. H. and A. B. Reinmann. 2011. Multi-factor global change experiments: what have we learned about terrestrial carbon storage and exchange? New Phytologist **192**:797-800.

Thomsen, C., G. Barbe, W. Williams, and M. George. 1986. "Escaped" artichokes are troublesome pests. California Agriculture **40**:7-9.

Thomsen, M. A. and C. M. D'Antonio. 2007. Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability, and environmental gradients. Oikos **116**:17-30.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

Tilman, D. 1988. Monographs in Population Biology No. 26. Plant Strategies and the Dynamics and Structure of Plant Communities. Tilman, D. Monographs in Population Biology, No. 26. Plant Strategies and the Dynamics and Structure of Plant Communities. Xi+360p. Princeton University Press: Princeton, New Jersey, USA. Illus:XI+360P.

Tilman, D. 1990. Constraints and Tradeoffs - toward a Predictive Theory of Competition and Succession. Oikos **58**:3-15.

Tilman, D., C. L. Lehman, and C. J. Yin. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. American Naturalist **149**:407-435.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Tognetti, P. M. and E. J. Chaneton. 2012. Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. Biological Invasions **14**:2531-2544.

Tognetti, P. M., E. J. Chaneton, M. Omacini, H. J. Trebino, and R. J. C. Leon. 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. Biological Conservation **143**:2494-2503.

Traveset, A. and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution **21**:208-216.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos **88**:225-238.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology **91**:2833-2849.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems **1**:511-523.

Turpie, J. K., C. Marais, and J. N. Blignaut. 2008. The working for water programme: Evolution of a payments for ecosystem services mechanism that addresses both poverty and ecosystem service delivery in South Africa. Ecological Economics **65**:788-798.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters **11**:1351-1363.

UNEP-SCBD. 2001. Global Biodviersity Outlook. UNEP Secretariat of the Convention on Biological Diversity, Montreal, Canada.

van der Heijden, M. G. A. 2004. Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. Ecology Letters **7**:293-303.

van der Putten, W. H., J. N. Klironomos, and D. A. Wardle. 2007. Microbial ecology of biological invasions. Isme Journal **1**:28-37.

Vasquez, E., R. Sheley, and T. Svejcar. 2008. Creating Invasion Resistant Soils via Nitrogen Management. Invasive Plant Science and Management **1**:304-314.

Vila, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarosik, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pysek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Vinton, M. A. and E. M. Goergen. 2006. Plant-soil feedbacks contribute to the persistence of Bromus inermis in tallgrass prairie. Ecosystems **9**:967-976.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997a. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications **7**:737-750.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997b. Introduced species: A significant component of human-caused global change. New Zealand Journal of Ecology **21**:1-16.

Vitousek, P. M. and L. R. Walker. 1989. Biological Invasion by Myrica-Faya in Hawaii - Plant Demography, Nitrogen-Fixation, Ecosystem Effects. Ecological Monographs **59**:247-265.

Vivrette, N. J. and C. H. Muller. 1977. Mechanism of invasion and dominance of coastal grassland by Mesembryanthemum crystallinum. Ecological Monographs **47**:301-318.

Vogelsang, K. M. and J. D. Bever. 2009. Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. Ecology **90**:399-407.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setala, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science **304**:1629-1633.

Wedin, D. A. and D. Tilman. 1990. Species effects on nitrogen cycling-a test with perennial grasses Oecologia **84**:433-441.

Weiher, E. and P. A. Keddy. 1995. Assembly Rules, Null Models, and Trait Dispersion - New Questions From Old Patterns. Oikos **74**:159-164.

Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient poor grasslands for a threatened species. Conservation Biology **13**:1476-1486.

Whisenant, S. 1999. Repairing Damaged Wildlands: A Process-Oriented, Landscape Scale Approach. Cambridge University Press, Port Chester, NY.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pages 4-10 *in* Symposium on Cheatgrass Invason, Shrub Die-Off, and other Aspects of Shrub Biology and Management, Las Vegas, NV.

White, P. S. and A. Jentsch. 2004. Disturbance, Succession, and Community Assembly in Terrestrial Plant Communities. Pages 342-366 *in* V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Island Press, Washington, DC.

Williams, P. A. and B. J. Karl. 2002. Birds and small mammals in kanuka (Kunzea ericoides) and gorse (Ulex europaeus) scrub and the resulting seed rain and seedling dynamics. New Zealand Journal of Ecology **26**:31-41.

Williamson, M. 1996. Biological Invasions. Chapman & Hall, Cornwall.

Wojterski, T. W. 1990. Degradation stages of the oak forests in the area of Algiers Vegetatio **87**:135-143.

Wolfe, B. E. and J. N. Klironomos. 2005. Breaking new ground: Soil communities and exotic plant invasion. Bioscience **55**:477-487.

Yelenik, S. G., W. D. Stock, and D. M. Richardson. 2004. Ecosystem level impacts of invasive Acacia saligna in the South African fynbos. Restoration Ecology **12**:44-51.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community Succession and Assembly: Comparing, Contrasting and Combining Paradigms in the Context of Ecological Restoration. Ecological Restoration **19**:5-18.

Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.

Yu, D. W. and H. B. Wilson. 2001. The competition-colonization trade-off is dead; Long live the competition-colonization trade-off. American Naturalist **158**:49-63.

Zavaleta, E. 2000. The economic value of controlling an invasive shrub. Ambio **29**:462-467.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16**:454-459.

Zeglin, L. H., M. Stursova, R. L. Sinsabaugh, and S. L. Collins. 2007. Microbial responses to nitrogen addition in three contrasting grassland ecosystems. Oecologia **154**:349-359.

Zobel, K., M. Zobel, and R. K. Peet. 1993. Change in pattern diversity during secondary succession in Estonian forests Journal of Vegetation Science **4**:489-498.

Zouhar, K., J. K. Smith, S. Sutherland, and M. L. Brooks. 2008. Wildlan fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42-vol 6. pp. 7-32. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, UT.

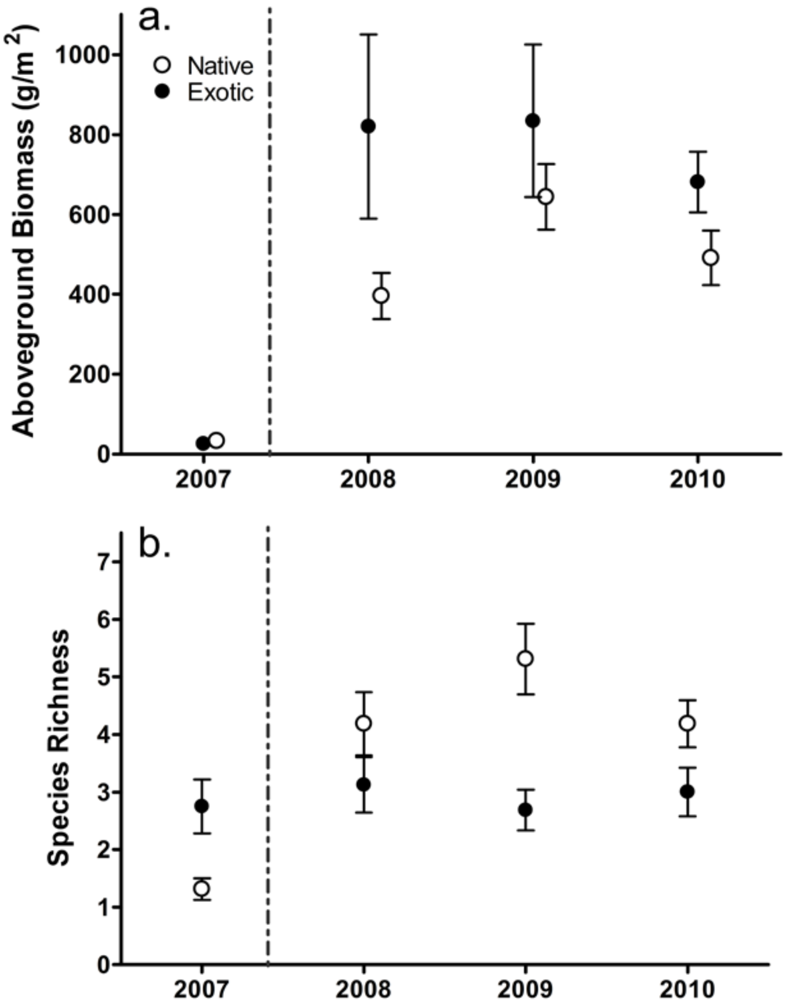
Appendix 1. Summary of parameter estimates (± 1 SE) for the allometric relationships used to estimate *Stipa pulchra* seedling and adult aboveground biomass. Relationships were fit within each resource treatment, if possible. Reported R^2 values are adjusted for those models with multiple predictor variables.

		Nitrogen Resource Treatment		
Stipa life stage	Predictor Variable	Low N	Ambient	High N
Seedling	Total No. Leaves	0.19 ± 0.05	0.36 ± 0.11	0.12 ± 0.02
	Height	0.122 ± 0.03		0.063 ± 0.02
	Total Leaves x Height	-0.03 ± 0.01		
	Intercept	-6.18 ± 0.30	-6.27 ± 0.85	-5.54 ± 0.35
R^2		0.80	0.72	0.86
Adult	No. of Culms		0.62 ± 0.08	
	Intercept		1.58 ± 3.05	
R^2			0.76	

Appendix 2. List of species occurring within each vegetation type during the course of the study. Dominant species were present 20% or greater abundance each year. A subdominant was present with abundances between 1-20%. A rare species was present with a maximum abundance of 1%. Family names in parenthesis; * indicates native species.

Species Groupings	Pre-Fire Patch Type	
	Native	Exotic
Dominant	*Stipa pulchra* (Poaceae)* *Avena fatua* (Poaceae) *Festuca perenne* (Poaceae)	*Avena fatua* *Bromus diandrus*
Subdominant	*Amsinckia menziesii* (Boraginaceae)* *Brassica nigra* (Brassicaceae) *Bromus diandrus* (Poaceae) *Bromus hordeaceus* (Poaceae) *Calystegia macrostegia* (Convolvulaceae)* *Cryptantha clevelandii* (Boraginaceae)* *Dichelostemma capitatum* (Liliaceae)* *Erodium cicutarium* (Geraniaceae) *Hemizonia fasciculata* (Asteraceae)* *Lupinus microcarpus* (Fabaceae)* *Lupinus succulentus* (Fabaceae)* *Picris echioides* (Asteraceae) *Stachys spp.* (Lamiaceae)* *Sysrinchium bellum* (Iridaceae)*	*Brassica nigra* *Bromus madritensis* *Erodium cicutarium* *Hordeum murinum* (Poaceae) *Festuca perenne* *Malva parviflora* (Malvaceae) *Medicago spp* (Fabaceae)
Rare	*Bromus carinatus* (Poaceae)* *Bromus madritensis* (Poaceae) *Calindrinia ciliata* (Polygonaceae)* *Calochortus catalinea* (Liliaceae)* *Calochortus splendens* (Liliaceae)* *Ericameria palmeria* (Asteraceae)* *Lasthenia californica* (Asteraceae)* *Sanicula spp.* (Apiaceae)*	*Amsinckia menziesii** *Dichelostemma capitatum** *Lupinus succulentus** *Cryptantha clevelandii**

Appendix 3. Aboveground biomass and species richness (mean ± 1SE) of native and exotic patches over time (n=8, at each time point; disturbance indicated by vertical dashed line).



Appendix 4. Total biomass for *Stipa pulchra* (a) and *Avena fatua* (b) individual summarized in above and belowground biomass across soil inocula and competition treatments. Means ± 1SE.