AN ABSTRACT OF THE DISSERTATION OF

Angela J. Brandt for the degree of Doctor of Philosophy in Zoology presented on March 14, 2011.

Title: The Roles of Provenance and Phylogeny in Recruitment, Community Assembly, and Species Coexistence in Invaded California Grasslands

Abstract approved:

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Biological invasions pose one of the greatest threats to global biodiversity, but many naturalized invaders coexist with the native community. Community ecology theory provides a framework for understanding the mechanisms by which invaders might coexist with native species or exclude them from the community, thus informing management practices to maximize their effectiveness at conserving native biodiversity. Differences in functional or phylogenetic similarity of invaders to native residents can affect invasion success and the probability they will coexist with natives. For example, functionally dissimilar species may not compete strongly and distantly related species may share fewer natural enemies. Furthermore, environmental heterogeneity can promote species coexistence by providing the opportunity for a greater number of coexistence mechanisms to operate, thereby mitigating the potential for species invasions to lead to native extinction.

My thesis examines how provenance (i.e., native origin) and phylogenetic relatedness of plant species affect community dynamics and species interactions in the invaded California grasslands. To do this I have assembled two unique community data sets, one spanning 48 years across a 1000-ha site and one spanning 7 years along a 500-km latitudinal transect. I show that native and exotic species abundance and diversity is highly variable in both time and space, but these provenance group responses are rarely negatively correlated (Chapter 2). Thus, exotic species do not generally appear to exclude natives from communities. Long-term abundance patterns further suggest that the system remains in a state of transience, and populations of several native species are declining at local scales (Chapter 3). Recruitment limitation due to the build-up of plant litter associated with exotic grasses may be generally responsible for these declines, but habitat suitability, land-use history, and community composition also affect native recruitment. Across the grasslands, disturbance and resource supply can interact to affect both species and phylogenetic diversity (Chapter 4). Disturbance in particular can increase diversity, likely by increasing opportunities for colonization by removing plant litter that previously limited recruitment. Both phylogeny and provenance can also affect biotic interactions, such as with communities of soil organisms (Chapter 5). Thus, I have shown that spatio-temporal heterogeneity, alterations to the biotic environment mediated by exotic invasion, and phylogenetic relationships among species are all important considerations when evaluating impacts of invasion and designing management strategies to conserve native biodiversity, especially in light of anthropogenic influence on disturbance regimes and resource supply.

The Roles of Provenance and Phylogeny in Recruitment, Community Assembly, and Species Coexistence in Invaded California Grasslands

by
Angela J. Brandt

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March 14, 2011
Commencement June 2011

Doctor of Philosophy dissertation of Angela J. Brandt presented on March 14, 2011.

APPROVED:

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Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Angela J. Brandt, Author

ACKNOWLEDGEMENTS

I owe so much to my advisor, Eric Seabloom. There is something special about being a professor's first doctoral student, and we learned a lot together along the way. Eric always pushed me to succeed and provided the valuable guidance and enthusiasm to help me get there. He is largely responsible for my development as a scientist and I am very happy with what I have accomplished thanks to him. My thesis committee has been incredibly supportive and a pleasure with whom to interact. Sally Hacker graciously stepped in to be my on-site advisor when Eric moved away, going above and beyond the call of duty to ensure I was taken care of in every way. Bruce McCune has provided important advice and feedback on statistical analysis and approaching ecological ideas from multiple perspectives. John Lambrinos was a great source of ideas and encouragement. Doug Johnson was a supportive graduate council representative.

My success with research and graduate school in general would not have been possible without the support of the Borer-Seabloom lab. Elizabeth Borer was always willing to provide feedback on my work, help manage finances, and lend her general support to my endeavors. I am so thankful that Cara Benfield and Sean Moore began the adventure of starting the B-S lab with me; I couldn't have asked for a better academic brother and sister with whom to learn the ropes. Phoebe Zarnetske, Kelly Farrell, Wendy Phillips, Tony Graziani, Joe Dauer, and Lydia O'Halloran were great at helping me prepare for oral exams, conference presentations, and research in general; I also thank all their partners for being great honorary lab members. Burl

Martin, Emily Orling, and Shawn Gerrity were instrumental in helping me with field and lab work, and were always willing to lend an ear and some advice when I needed it. I could never have finished data collection without the assistance of field crews and lab assistants, especially Vince and Autumn Adams, Travis Lewis, Greg Creager, and Maya Villereal. I also want to thank my honorary lab, the Cadotte lab at the University of Toronto at Scarborough, for so quickly bringing me into the fold during my short stay in Toronto. Marc Cadotte has been a wonderful collaborator, his family was incredibly welcoming and hospitable, and his lab members and associates continue to be supportive both in research and in friendship.

Field work would not have been possible without the amazing infrastructure of the University of California’s Natural Reserve System, and would not have been nearly as feasible nor as enjoyable without the friendship and support of the staff at Sedgwick, Hastings, and McLaughlin reserves. I would especially like to thank Mark Stromberg, Jaime del Valle, Walt Koenig, Eric Walters and family, and all the other researchers at Hastings for making it like a second home to me. Cathy Koehler and Paul Aigner at McLaughlin were incredibly patient and supportive, and Kate McCurdy and Barbara Huebel at Sedgwick have been great. I will miss spending springtime in California. Thanks also to Susi Bradley, Kevin Meehan, and the O’Briens for helping me easily access field plots on their land.

Many thanks go to the Zoology department for supporting its graduate students and for maintaining such a strong sense of community. Thanks especially to Tara Bevandich, Torri Givigliano, and Traci Durrell-Khalife for caring so much and always helping me with the many logistical issues that pervaded my graduate career. Thanks to Bruce Menge and Joe Beatty for being great department chairs. Thanks also, Joe, for working so hard to keep me supported financially and academically throughout my time at OSU. Doug Warrick was a great colleague who could always make me laugh; thanks for your constant support during my teaching and grad career at OSU.

There is not enough space or time for me to adequately thank Zo-grads for being such an amazing group of people and friends. I can’t imagine surviving grad school without the support and input of such a motivated, intelligent, and fun community of grads. I would especially like to thank Betsy Bancroft for being an amazing mentor and role model—from teaching, to research, to building confidence and managing so many tasks, she was always willing to play the role of senior grad student for me when I didn’t have one to whom to turn in my own lab. Karen Kiemnec-Tyburczy, Barbara Han Ng, and Laura Petes were also great mentors and friends. Thanks also to my cohort and other close friends in the department, including Catherine Searle, Dafne Eerkes-Medrano, Lindsay Biga, Julia Buck, Joe Tyburczy, Mark Christie, Jacob Tennessen, Kaitlin Bonner, and Josef Uyeda. A big thank you to all my wonderful friends on my indoor soccer teams, in the Corvallis swing dance community, and in the Coalition of Graduate Employees for your support. Thank you, Laura Cole, for our annual low-budget adventures to provide a much-needed break from work. And to my stellar roommates, Sarah Eddy and Chris Friesen: you are the best, and thanks for keeping me sane, making me laugh, and reminding me that I could do it. I promise to overturn the paradigm.

My family has loved and supported me throughout my life and I greatly appreciate that. I regret that my grandmother, Marie Brandt, and great aunt, Marylea Ewald, passed away before seeing me earn my doctorate, but I thank them for always believing in me. I am grateful for the continued support of my grandmother, Ann Wagner, who has always strongly supported female independence and pursuit of advanced degrees, and my great aunt, Mary Jean Peterson. Finally, a heartfelt thank you to my mother, Jeanette Brandt, who has always been my biggest fan, my best friend, and my hero. I would never have gotten to where I am today without her unconditional, unyielding support and love. She always put me first, pushed me to succeed, promoted my independence, and convinced me that I could do anything. She is an inspiration as a parent and friend; thank you, Mom, for being you.

CONTRIBUTION OF AUTHORS

Chapter 4: Dr. Marc Cadotte provided critical assistance with constructing the phylogenetic tree and phylogenetic diversity analyses, as well as providing valuable input on the shaping and writing of the manuscript.

Chapter 5: Dr. Parviez Hosseini applied plant data to mathematical models to obtain growth rate responses and provided valuable input to writing of the manuscript.

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DEDICATION

This dissertation is dedicated to my mother, Dr. Jeanette A. Brandt.

The Roles of Provenance and Phylogeny in Recruitment, Community Assembly, and Species Coexistence in Invaded California Grasslands

1 – General Introduction

One of the most fundamental goals in community ecology is to clarify the mechanisms governing species coexistence and ultimately community diversity (Hutchinson 1959). Developing and improving community ecology theory and predictions regarding species coexistence has important implications for conservation in the face of global change, including invasions by exotic species and anthropogenic effects on disturbance regimes and resource supply within ecosystems. Biological invasions pose one of the greatest threats to global biodiversity and management of invasions requires significant economic resources (Stein et al. 2000, Mace et al. 2005, Pimentel et al. 2005). Applying ecological theory to environmental problems, such as invasions, can provide a framework to understand and predict the potential impacts of global change on biodiversity and ecosystem processes (Shea and Chesson 2002). A clear understanding of the drivers of community diversity can inform ecosystem management to increase the effectiveness of conservation and restoration efforts.

Environmental heterogeneity can promote species coexistence by allowing species to take advantage of unfavorable conditions for their competitors to bolster their own population growth (reviewed in Chesson 2000). Recent work suggests that as environmental heterogeneity increases communities may be more subject to successful invasions, but those invasions are less likely to lead to species extinctions (Melbourne et al. 2007). The role of environmental heterogeneity in species coexistence may explain the apparent paradox of native-exotic diversity relationships, which tend to be negative at small spatial scales but positive at large scales (Davies et al. 2005, Fridley et al. 2007). In Chapter 2, I explore large-scale, long-term spatio-temporal patterns of native and exotic plants in the California grasslands to quantify the magnitude of variation in community patterns and the similarity of native and exotic species responses. Though these grasslands experienced a dramatic invasion of Eurasian annual grasses and forbs that occurred over 250 years ago (Heady 1977, Hamilton 1997a, Mensing and Byrne 1998), native and exotic abundance and diversity continue to show high variability over time and space, suggesting that the system is still in a state of transience. Effects of both spatial and temporal heterogeneity should be considered simultaneously because spatial relationships between native and exotic diversity are temporally variable. Overall, native and exotic species groups appear to respond similarly to variability in the environment, thus exotic species may not generally exclude native species from this system. Further examination of the mechanisms by which exotic species might reduce native diversity and improving predictions of which species will be most affected is important to identify how limited management resources can be used most effectively.

The effects of invasions on biodiversity vary with spatial scale such that regional diversity may increase following invasion, but temporal changes in native and exotic diversity over a range of scales are rarely documented (Sax et al. 2002, Davis 2003). Using long-term data on local species abundances can aid in determining the roles of recruitment limitation processes that may be driving local species declines.

Recruitment into a community can be propagule- and/or establishment-limited (Clark et al. 2007), which can limit local population size and persistence. Maintenance of local populations is often critical for species persistence (Hanski et al. 1996), thus evaluating how monitoring data can inform understanding of local species declines has important implications for management of biodiversity. In Chapter 3, I examine the roles of propagule-limitation, habitat suitability, and biotic interactions on recruitment of native species that had declined in abundance in long-term monitoring plots within one California grasslands site. Native plant recruitment is both propagule- and establishment-limited, but the primary mechanism by which exotic species impact native recruitment is through the build-up of litter. The effects of biotic interactions on plant recruitment vary with land-use history, however, such that anthropogenic effects on disturbance regimes, such as through livestock grazing, can influence the effect of exotic species on natives.

Recruitment to communities through dispersal and establishment processes determines community diversity (Keddy 1992, Weiher and Keddy 1995), and disturbance and resource supply can either increase or decrease diversity through their effects on mechanisms of community assembly (Petraitis et al. 1989, Foster and Gross 1998, Chase 2007, Hillebrand et al. 2007, Chase 2010). Our understanding of how these processes affect diversity has become increasingly important given anthropogenic modification of disturbance regimes and nutrient cycling (Weiss 1999, Fenn et al. 2003, Hayes and Holl 2003a). The concept of community diversity has recently been broadened to include species' evolutionary relationships, because these relationships likely incorporate information about ecological similarity among species that can improve predictions of community responses to assembly mechanisms (Webb et al. 2002, Cavender-Bares et al. 2009). In Chapter 4, I examine the effects of disturbance and nitrogen supply on local community diversity in California grasslands and variation in community composition across the region. I use both species diversity and phylogenetic diversity metrics to evaluate the potential roles of various community assembly mechanisms in governing diversity. In general, these grassland communities may be structured more by environmental filtering than other assembly processes, where resident communities limit colonization by additional species. Disturbance appears to affect community diversity more strongly than nitrogen supply, and likely increases opportunities for colonization that lead to increased species and phylogenetic diversity both within local communities and across the region. However, incorporating phylogenetic relationships to provide insight into mechanisms structuring communities is only useful if those relationships correspond to traits on which these mechanisms might act (Cavender-Bares et al. 2009). Exploring the roles of additional biotic interactions that may structure communities would further elucidate the mechanisms governing diversity.

Community ecology often focuses on aboveground biotic interactions that can structure communities, however interactions between above- and belowground biological communities also may drive community dynamics (Wardle et al. 2004).

Plants may alter soil communities with the potential to impact other plant competitors through feedback loops (Bever et al. 1997, Bever 2003). Interactions with soil communities can promote species coexistence by reducing performance of dominant species (e.g., Bever et al. 1997, Bever 2003) and may facilitate invasion when exotics lose natural enemies and/or gain mutualists in their introduced range (Callaway et al. 2003, Mitchell et al. 2006, Van der Putten et al. 2007). Phylogenetic relationships between plants may affect the impact of soil communities on coexistence and invasion because exotics more closely related to natives may be more likely to gain soil pathogens and/or mutualists in their introduced range (Richardson et al. 2000, Agrawal et al. 2005, Mitchell et al. 2006). In Chapter 5, I explore the potential for soil biota to affect California grassland community dynamics by evaluating whether the performance of native and exotic grasses is strongly and differentially affected by soil biota. Phylogenetic relationships best explain variation in plant resource capture, resource allocation, and growth rate, while soil biota are a good predictor of resource capture. Furthermore, both phylogenetic relationships and life history/provenance can predict plant responses to soil communities. Thus, both phylogeny and provenance should be considered when determining the mechanisms governing species coexistence and how communities respond to altered ecosystem processes.

2 – Regional and decadal patterns of native and exotic plant coexistence in California grasslands

Angela J. Brandt and Eric W. Seabloom

Ecological Applications
In press

ABSTRACT

Coexistence through a variety of mechanisms is possible for species with differential responses to environmental conditions. Understanding the role of environmental heterogeneity in mediating coexistence of species of different provenance (i.e., native versus exotic) has important implications for theory and management. We used two California grassland data sets, one spanning 7 years at three reserves along a 500-km latitudinal gradient and one spanning 48 years at 11 sites within a single 1000-ha reserve, to determine how environmental heterogeneity in space and time contribute to variability in provenance group abundance and diversity, and whether native and exotic species respond similarly to spatial and temporal variability. We found that temporal environmental heterogeneity is the primary determinant of provenance group abundance, while spatial and temporal environmental heterogeneity both contribute to community diversity. Spatial and temporal heterogeneity must therefore be considered simultaneously when examining community dynamics and species coexistence. Provenance was a poor general predictor of species response; native and exotic species exhibit similar spatio-temporal patterns in some cases but not others. Plant persistence may depend more upon the abiotic environment than competition from the other provenance group as native and exotic diversity were generally positively correlated. Furthermore, mesoscale (10^2-10^3 m) spatial heterogeneity may be a greater mediator of provenance group coexistence than temporal heterogeneity or spatial heterogeneity at other scales.

2.1 INTRODUCTION

Environmental heterogeneity can promote species coexistence by allowing species to take advantage of conditions that are unfavorable for their competitors (reviewed in Chesson 2000). Spatial and temporal heterogeneity in abiotic environmental conditions, such as microtopography and climate, have each been shown to promote species coexistence (Vivian-Smith 1997, Adler et al. 2006). This strong body of community ecology theory has important implications for invasion ecology theory and application. Environmental heterogeneity can increase the maximum potential species diversity in a community and allow novel species to invade more successfully (Melbourne et al. 2007). Additionally, native species may be better able to persist in heterogeneous than in homogeneous environments due to availability of a greater number of potential coexistence mechanisms, thereby lessening the impact of invasion in terms of species displacement (Melbourne et al. 2007). Understanding the effect of heterogeneity on the processes that lead to coexistence can inform management of invaded ecosystems. For example, such information may allow managers to focus their limited resources on restoration efforts in locations or time periods where native species performance is maximized or on control of exotic invaders where they have the greatest negative impact on native species.

Examining spatial and temporal variability in the composition of invaded plant communities may provide insight into how species of different provenance (i.e., native and exotic) use environmental heterogeneity to coexist. Diversity of native and exotic species tends to be negatively correlated at fine spatial scales and positively correlated at coarser scales (Fridley et al. 2007), suggesting that natives and exotics are better able to coexist at coarser scales. Increases in environmental heterogeneity with increasing spatial scale is one explanation for this complex native-exotic diversity relationship (Davies et al. 2005). The influence of temporally heterogeneous environmental conditions on relationships between native and exotic species has received less attention but may also promote their coexistence, particularly when crucial life history traits, such as seed dormancy and germination cues, differ between natives and exotics (Levine and Rees 2004). Fewer studies have compared the relative effects of spatial and temporal heterogeneity on species diversity (e.g., Adler and Levine 2007), and none to our knowledge have done so in an invasion context. Here we concurrently examine spatial and temporal variability of native and exotic species in California grassland communities to explore how environmental heterogeneity may affect community dynamics and whether provenance group differences may promote their coexistence.

California grasslands are a particularly interesting system in which to examine the effects of spatio-temporal environmental heterogeneity on coexistence of native and exotic plants because of the spatial extent and duration over which the native and exotic flora have coexisted. This system has experienced a dramatic, historical invasion in which over 9 million hectares is currently dominated by Eurasian annual grasses and forbs that primarily invaded in the mid-1800s (Heady 1977). Few region-wide extinctions of native plant species have occurred in the face of this invasion, however, suggesting that natives are coexisting with the exotic invaders, at least at some spatial scales (Stein et al. 2000, Seabloom et al. 2003b, 2006). Although the relative importance of spatially and temporally heterogeneous conditions and the relevant scale at which to examine effects of heterogeneity remain unclear, environmental heterogeneity likely plays a strong role in native-exotic coexistence processes in this system. Native species' adaptations to harsh soil conditions (Seabloom et al. 2003a, Davies et al. 2005) and difficulty re-colonizing sites subjected to certain types of anthropogenic disturbance (Stromberg and Griffin 1996) suggest that spatial mechanisms of coexistence are important. Temporal mechanisms may also be important, however, as interannual variation in the dominance of different plant groups is related to climatic patterns (Pitt and Heady 1978) and high levels of temporal environmental heterogeneity may promote persistence of rare native forbs (Levine and Rees 2004).

Here, we examine spatio-temporal patterns in native and exotic abundance and diversity using two large-scale plant community data sets in California grasslands as evidence for spatial and temporal mediation of native-exotic coexistence and discuss the implications of these patterns for research and management. Our objectives are to determine (1) the relative magnitude of spatial and temporal variation in native and exotic abundance and diversity and (2) whether native and exotic species respond similarly to spatial and temporal variability.

2.2 METHODS

We used two large-scale data sets of grassland community composition, one spanning 7 years across three reserves situated along a 500-km latitudinal gradient and one spanning 48 years at 11 sites within a single 1000-ha reserve, in the University of California's Natural Reserve System to quantify spatio-temporal patterns in native and exotic plant abundance and diversity. The first data set (hereafter the "multi-site data set") was part of a seed-addition experiment established at Sedgwick Reserve, Santa Barbara County (34º42´N, 120º2´W); Hastings Natural History Reservation (HST), Monterey County (36º22´N, 121º32´W); and McLaughlin Natural Reserve, Napa/Lake/Yolo Counties (38º52´N, 122º25´W), California, USA (Seabloom 2011). These reserves span a 500-km latitudinal gradient and nearly a two-fold precipitation gradient, with Sedgwick receiving 380 mm/year, Hastings 530 mm/year, and McLaughlin 620 mm/year on average. In fall 2003, we established plots in a nested sampling design at three spatial scales (Fig. 2.1). At each of the three reserves, three blocks consisting of a 5×5 grid of 5×5-m plots were located in open canopy, annual grassland. We used data from a permanent ½×1-m quadrat within the lower left subplot of each of four randomly selected plots within each block, which were unmanipulated experimental controls from a separate study, for a total sample size of

36 (n=35 in 2005 and 2006, due to missing data). Percent cover of each plant species was visually estimated during peak biomass (April-June) of 2004-2010 and summed by provenance group to estimate native and exotic abundance. Total cover sums to more than 100% in areas with multi-layer canopies. Native and exotic diversity was calculated as richness of each provenance group in each quadrat.

The second data set (hereafter the “long-term data set”) was part of a grazing-effects study established at HST in 1963 and sampled from 1963-66, 1978, and 2005-2010. The sampling design consisted of 11 blocks established along the boundary of the 1000-ha reserve in a range of open canopy to oak woodland habitats to monitor understory plant community composition. Presence of each species was recorded in 20 to 120 20×50-cm quadrats regularly spaced throughout each block during peak biomass (April-June). Block-level native and exotic abundance was estimated as the summed frequency of species in each provenance group in each block, where frequency is the number of quadrats in which a species was observed divided by the total number of quadrats sampled. Block-level diversity was estimated as the bootstrapped mean richness of native and exotic species observed in 20 randomly selected quadrats in each block, with 1000 iterations. Percent cover of each species was also recorded in three ½×1-m quadrats located at the ends and center of a 40-m transect located in each block in 2006-2009. Results from these data were similar to the long-term data from smaller quadrats, thus only results from the long-term data are discussed here (see *Appendices A-C*).

All statistical analyses were performed in R version 2.9.0 (R Development Core Team 2010). We performed variance components analyses (VCA) to determine the relative effects of space and time on native and exotic abundance and diversity, and on the log ratio of native to exotic responses to determine whether these provenance groups varied similarly in space and time. Log ratios were calculated as ln([native response + 0.1] / [exotic response + 0.1]) for each plot in the multi-site data set and as ln(native response / exotic response) for each block in the long-term data set. We used nested random effects models of year within plot within block within site for the multi-site data set and year within block for the long-term data set to determine the proportion of the variance in native and exotic responses explained by each level of time (year) and space (site, block, and plot) using the nlme library in R (Pinheiro and Bates 2000, Crawley 2007). We also examined native-exotic diversity relationships across space and time using a multiple linear regression. A model of exotic richness regressed on native richness and the year of sampling, including the interaction of these two variables, was produced at each of the three spatial scales (plot, block, and site) in the multi-site data set. For this analysis, we used total richness of each provenance group at each scale to compare the relationships in different years.

To corroborate results from the analyses described above with a spatially-explicit analysis, we used the spline correlogram as described by Bjørnstad and Falck (2001) and applied to these grassland systems by Seabloom *et al.* (2005) to describe spatial autocorrelation in abundance and diversity of each provenance group and spatial covariance between the groups in the multi-site data set. We calculated geographical distance between plots (i.e., spatial lags) using UTM coordinates obtained for each plot with a Garmin eTrex Venture (Garmin International, Inc., Olathe, Kansas, USA). For all correlograms, we used df = 6, a maximum lag of 300 km, and 1000 permutations to calculate 95% confidence envelopes through bootstrapping. We chose our maximum lag to allow comparisons among adjacent reserves while maintaining a greater number of correlations for the analysis; using a maximum lag of 7 km to limit comparisons to the within-reserve scale did not affect the results. To determine spatial autocorrelation of native and exotic plants, we estimated the value of the spatial autocorrelation function at a lag of 0 m for each response variable using a univariate spline correlogram. To determine spatial covariance of the provenance groups, we estimated the value of the spatial cross-correlation functions between native and exotic abundance and native and exotic diversity at a lag of 0 m using univariate spline cross-correlograms. We produced seven spline correlograms and cross-correlograms for each response and provenance group combination—one for each individual year's data and one for responses averaged over 7 years—to examine whether spatial patterns varied over time.

2.3 RESULTS

In the multi-site data set, native plants were less abundant and diverse than exotics (log ratios < 0), with responses of provenance groups varying strongly and somewhat idiosyncratically over time (Fig. 2.2 and 2.3). We were able to classify 67-100% of species in each multi-site data set quadrat as “native” or “exotic”, with an average of 97%; 50-100% of species in each quadrat were annuals, with an average of 92%. In the long-term data set, native and exotic plant abundances at the block level were generally similar, with high interannual variability (Fig. 2.4 and 2.5, top panels). However, a trend toward exotic dominance was observed over the course of the long-term data set (Fig. 2.5, top panel). Native diversity was consistently greater than exotic diversity, with little variation over time (Fig. 2.4 and 2.5, bottom panels). We were able to classify 91-100% of species in each block as “native” or “exotic”, with an average of 98%; 45-87% of species in each block were annuals, with an average of 67%.

2.3.1 Relative Effects of Space and Time

In the multi-site data set, over 93% of the variability in native abundance and 99% of the variability in exotic abundance was accounted for by space (site, block, and plot) and time (year) variables, with year being the most important factor (Fig. 2.6, top left). Over 91% of the variability in native and exotic diversity was accounted for by space and time variables, with year being the most important factor for exotic diversity and block and year accounting for similar proportions of the variation in native diversity (Fig. 2.6, top right). The spatial scale accounting for the greatest amount of variation in provenance group abundance and diversity was the block scale, or within-site variability. Distance between blocks ranged from 291 – 6957 m (mean =

2429 m). Spatial autocorrelations corroborated these trends. The magnitude of spatial autocorrelation of the provenance groups' abundance and diversity varied from year to year (Table 2.1), supporting VCA results that time accounts for a large proportion of variability in responses. Generally, provenance group responses, especially for natives, were positively spatially autocorrelated (Table 2.1), supporting VCA results that variability within blocks (i.e., at the plot scale) was low.

In the long-term data set, over 91% of the variability in native abundance and over 88% of the variability in exotic abundance were accounted for by space and time variables, with year being the more important factor, especially for exotics (Fig. 2.6, bottom left). Over 92% of the variability in native and exotic diversity was accounted for by space and time variables, with block being the more important factor (Fig. 2.6, bottom right).

2.3.2 Similarity of Provenance Group Responses

In the multi-site data set, over 92% of the variability in the log ratio of native to exotic abundance was accounted for by space and time variables (Fig. 2.6, top left). Year accounted for less variability in log ratios of abundance than native or exotic abundance alone, suggesting provenance group abundance varied similarly over time. Over 99% of the variability in the log ratio of native to exotic diversity was accounted for by space and time variables, with year and block accounting for similar proportions of the variation (Fig. 2.6, top right).

In the multi-site data set, native and exotic diversity were positively related at all spatial scales (Fig. 2.7), though the strength of this relationship varied by both year and spatial scale (Table 2.2). At the plot and block scales, provenance group richness was positively related ($P = 0.009$ and 0.06, respectively), with the indication of an interaction for the 2008 data at the block scale ($P = 0.06$; see Table 2.2 and Fig. 2.7, middle panel). At the site-scale, no effect of year was observed and a simplified model including only richness demonstrated a significant positive relationship ($P < 0.0001$, adjusted $R^2 = 0.65$). Overall, both the variance component and regression analyses suggested that provenance group diversity varied most similarly at the site and plot spatial scales, and most idiosyncratically at the block scale and over time. Spatial cross-correlations corroborated these results. Native and exotic abundance and diversity did not significantly covary in general, but the strength and direction of their covariance differed by year (Table 2.1). Positive covariance in diversity was stronger than in abundance. Additionally, responses of both provenance groups tended to be positively spatially autocorrelated at the plot scale (Table 2.1). Thus, provenance groups exhibited similar responses on occasion but were not strongly synchronous in general.

In the long-term data set, over 92% of the variance in the log ratio of native to exotic abundance was accounted for by space and time variables (Fig. 2.6, bottom left). Year accounted for less variability in log ratios of abundance than native or exotic abundance alone, suggesting provenance group abundance varied similarly over time. Over 93% of the variance in the log ratio of native to exotic diversity was accounted for by space and time variables, with similar trends to those observed for native and exotic diversity alone (Fig. 2.6, bottom right). Thus, provenance group diversity did not appear to vary similarly over space or time.

2.4 DISCUSSION

2.4.1 Relative Effects of Space and Time

Community abundance and diversity had distinctly different spatial and temporal variability. Plant abundance was most strongly related to temporal environmental heterogeneity in our study, which is supported by other work (Chiarucci and Maccherini 2007, Hobbs et al. 2007, Laughlin and Moore 2009). Plant diversity, however, was most variable at intermediate scale (10^2 - 10^3 m) spatial environmental heterogeneity, with the relative importance of temporal heterogeneity varying among communities. Differences among communities may be due to differences in the magnitude of spatial heterogeneity, which may be positively related to diversity (Davies et al. 2005, but see Reynolds et al. 2007), or other community characteristics, such as the dominant life history. High temporal variation in diversity has been observed in annual (Elmendorf and Harrison 2009) and mixed annual and perennial grassland communities, with some perennial species exhibiting less interannual variation (Chiarucci and Maccherini 2007). Adler and Levine (2007) also observed greater spatial than temporal variability in diversity in predominantly perennial grassland communities.

2.4.2 Similarity of Provenance Group Responses

We found mixed evidence for similar responses to spatio-temporal environmental heterogeneity from native and exotic species. Native and exotic California grassland annual plants respond similarly to temporally varying climatic conditions (Elmendorf and Harrison 2009), which may explain the levels of temporal synchrony we observed in provenance group responses, as the majority of our species were annual. Whether provenance groups respond similarly in general to spatial environmental heterogeneity is unclear and may depend on the spatial scale and abiotic characteristics examined (Davies et al. 2005, Kumar et al. 2006). Seabloom (2011) found no effect of experimental disturbance and nitrogen treatments on native or exotic California grassland species cover. Here, native and exotic responses were most differentiated at intermediate spatial scales (i.e., within reserves), thus spatial environmental heterogeneity at this scale may be a greater mediator of coexistence between these groups than at other scales, and than temporal heterogeneity in certain communities. Both provenance groups were generally spatially aggregated (i.e., exhibited positive spatial autocorrelation), thus favorable abiotic environmental conditions (e.g., that enhance recruitment rates) for both groups are likely spatially heterogeneous and/or local seed dispersal is prevalent (Seabloom et al. 2005). The two provenances also generally exhibited positive or random spatial covariance, suggesting they may have similar habitat preferences (Seabloom et al. 2005, Adler and Levine 2007). Furthermore, negative spatial covariance would indicate that a group's success is maximized in the absence of the other group, likely due to competition (Seabloom et al. 2005). Taken together, results from our spline-correlogram analyses thus suggest that common abiotic conditions are generally more important to native and exotic community patterns than competition. This conclusion is supported by the positive native-exotic diversity relationships at all spatial scales in this study. The yearly variation we observed in spatial covariance and diversity relationships between groups may reflect temporal variation in competitive effects due to variability in productivity (Laughlin and Moore 2009, but see Elmendorf and Moore 2007) or favorable abiotic conditions (Elmendorf and Moore 2007, Elmendorf and Harrison 2009). Though native diversity has not declined over the timescales examined, it is unclear from the current study whether this is due to compensatory effects (Hobbs et al. 2007), elevated reproductive output in years with favorable conditions (Elmendorf and Harrison 2009), or insufficient timescales to detect declines. Thus, exotic species do not appear to be competitively excluding the contemporary native community as a whole within our sites, but heterogeneous abiotic conditions may be important to persistence of species from both provenance groups across the landscape. Future work comparing provenance group responses to abiotic environmental variables would provide additional evidence for this conclusion. Furthermore, the scope of our results here does not permit inference to the effect of exotic species on native abundance and diversity in the past, nor the potential for species-specific impacts of exotic invasion.

2.4.3 Research and Management Implications

This work shows that simultaneous consideration of spatial and temporal processes and explicit consideration of scale are important in both basic ecology and conservation planning. Spatial and temporal environmental heterogeneity may differentially affect community properties (Adler and Levine 2007, Chiarucci and Maccherini 2007), or interact in their effects (Laughlin and Moore 2009). For example, though we observed positive native-exotic diversity relationships at all spatial scales, these relationships varied among years and explained less variability in richness at finer scales than the coarsest scale. Furthermore, abundance and diversity of plant communities may be differentially affected by spatially heterogeneous abiotic conditions. For example, disturbance and nitrogen availability affected species richness but not cover of native and exotic species in California grasslands (Seabloom 2011). Observed spatio-temporal community patterns may be altered when including additional environmental variables in analyses (Fridley et al. 2007) or conducting studies over longer time scales (Hobbs et al. 2007), with implications for determining which processes may be driving these patterns. Additionally, high temporal variability in abundance we observed suggests that plant species rarity in one year may not indicate long-term declines and that multiple years of sampling may be required to detect certain species. Better general predictions of how environmental heterogeneity affects species coexistence may therefore require further examination of how different components of environmental heterogeneity affect various community properties, and exploration into which abiotic and biotic community characteristics determine community response to environmental heterogeneity. The ability to provide such predictions could be particularly useful in biodiversity management. For example, they may suggest in which communities, and for which species, restoration projects would most benefit from spreading seeding efforts over multiple years versus multiple sites, as well as suggesting the relevant scale at which to conduct management activities.

This work demonstrates a useful framework for suggesting whether to focus future research on abiotic or biotic factors as drivers of native species persistence, as well as indicating whether manipulations of seed supply, abiotic environmental conditions, or competition from exotics might be most effective for promoting native species diversity. For example, spatial aggregation of natives may indicate localized dispersal as well as spatial heterogeneity of favorable habitat and, coupled with random to positive covariance of native and exotic groups, corroborates other findings that seed addition of native species may be a viable restoration method where natives are currently absent (Seabloom et al. 2003a).

Our results also provide insight into the impact of exotic species on the native community. We show native and exotic diversity to be positively related, perhaps due to the promotion of both invasion and coexistence mechanisms by environmental heterogeneity in the system (Melbourne et al. 2007), but covariance in abundance of the two provenance groups at fine scales is highly variable over time. The primary impact of exotic species on natives at local scales may thus be to reduce their abundance rather than diversity, and further examination of the effects of low population size on persistence of native species and supplementary seeding of extant native populations may be important for their conservation. Furthermore, as we found no overall correlation between exotic abundance and richness at the plot scale (R = 0.072, P = 0.25), these patterns suggest that certain exotic species, perhaps those that persist at high abundances, may pose a greater threat to native persistence than diverse exotic communities. Species-specific patterns would provide further insight into how the impact of exotic species on natives varies with species identity as compared to abundance and diversity (Elmendorf and Moore 2007).

Grouping species by provenance as done here may not adequately capture ecological differences. For example, interannual variation in abundance of functional groups (grass, leguminous forb, and non-leguminous forb) may be related to temporally-varying climatic conditions (Pitt and Heady 1978). Additionally, life history may be a greater determinant of a species' environmental response, leading to aggregation of annual plants and their segregation from perennials (Seabloom et al. 2005). Spatial and temporal heterogeneity are the basis of the most robust diversity-maintaining mechanisms (Chesson 2000) and are thus critical to understanding the fate and implication of species invasions (Melbourne et al. 2007). However, provenance provides only a single axis along which species may differ in their responses to a varying environment. A full examination of species-specific patterns, including which species appear to drive the spatio-temporal patterns observed and the common traits of species with concordant environmental responses will ultimately be critical to interpreting spatio-temporal plant patterns and their implications for species coexistence and land management.

ACKNOWLEDGEMENTS

K. L. White generously provided his long-term data set from HST and M. R. Stromberg provided essential help in locating and continuing monitoring of these plots. We thank T. Yoshida, B. A. Martin, E. C. Orling, and research crews at OSU and University of California (UC) – Santa Barbara for field assistance. Thanks also to the UC Natural Reserve System and Sedgwick, Hastings, and McLaughlin Reserves. S. D. Hacker, K. A. Moore, and an anonymous reviewer provided helpful comments on the manuscript. Work funded by NSF DEB-0235624 (O. J. Reichman, J. Schimel, and E. W. Seabloom) and DEB-0910043 (E. W. Seabloom and A. J. Brandt), Andrew W. Mellon Foundation (O. J. Reichman and E. W. Seabloom), and UC Integrated Hardwood Range Management Program (W. D. Koenig, M. V. Ashley, E. T. Borer, J. M. H. Knops, E. W. Seabloom, and M. R. Stromberg).

Table 2.1: Spatial autocorrelation and covariance of the abundance and diversity of native and exotic plant species in grassland communities at reserves in California, USA.

	Abundance		Diversity	
	Native	Exotic	Native	Exotic
Spatial autocorrelation				
2004	0.41*	0.28	0.31	0.52*
2005	0.47*	0.22	0.57*	0.72*
2006	0.25	0.01	0.36	0.26
2007	0.38*	0.21	0.19	0.41
2008	0.21	0.06	0.24	0.03
2009	0.20	0.28	0.23	0.35
2010	0.13	0.27	0.39*	0.34
7-year average	0.44*	0.27	0.34*	0.50*
Spatial cross-correlation				
2004	0.31		0.38*	
2005	0.27*		0.59*	
2006	0.13		0.23	
2007	0.16		0.06	
2008	−0.15		−0.14	
2009	−0.29		0.19	
2010	−0.33*		0.31*	
7-year average	0.12		0.28	

Notes: Values were determined by intercepts of the spatial autocorrelation and cross-correlation functions. Autocorrelations and cross-correlations were calculated using univariate spline correlograms and cross-correlograms, respectively, with df = 6 and a maximum lag of 300 km for responses averaged over seven years and for each year individually. * $P < 0.05$ from 1000 bootstrapped samples.

Table 2.2: Relationship of native to exotic diversity at three spatial scales for seven years of sampling in grassland communities at reserves in California, USA.

Year	Plot-scale	Block-scale	Site-scale
2004	0.60	0.72	0.47
2005	0.60	0.32	0.88
2006	0.32	0.52	0.86
2007	0.38	0.31	1.46
2008	0.16	−0.04	2.00
2009	0.36	0.28	0.57
2010	0.42	0.25	0.86
Adjusted R^2	0.29	0.34	0.41

Notes: A nested sampling design was used, with four plots within each of three blocks at each of three sites. Sampling was conducted at three sites spanning a 500-km latitudinal gradient (i.e., site scale). At each site, three blocks consisting of a 5 × 5 grid of 5 × 5 m plots were established (i.e., block scale). A permanent 0.5 × 1 m quadrat within the lower left subplot of each of four randomly selected plots within each block was sampled to obtain data at the plot scale (see Fig. 2.1). Values presented are slopes from a multiple regression model at each scale of exotic richness on native richness and year, including an interaction of the two variables, and the adjusted R^2 for each model.

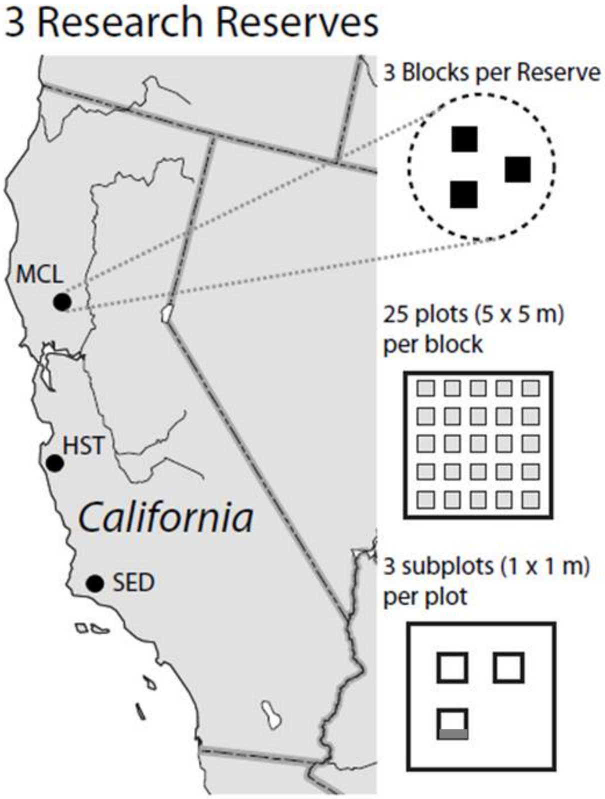


Figure 2.1: Nested design of the multisite data set for grassland plant community data from California, USA. At three sites (McLaughlin Natural Reserve [MCL], Hastings Natural History Reservation [HST], and Sedgwick Reserve [SED]), three blocks consisting of a 5 × 5 grid of 5 × 5 m treatment plots were established. Each plot contained three 1 × 1 m subplots, and data used here were from a permanent 0.5 × 1 m quadrat within the lower left subplot (gray rectangle) of each of four randomly selected plots within each block, which were unmanipulated experimental controls from a separate study. Modified with permission from (Seabloom 2011).

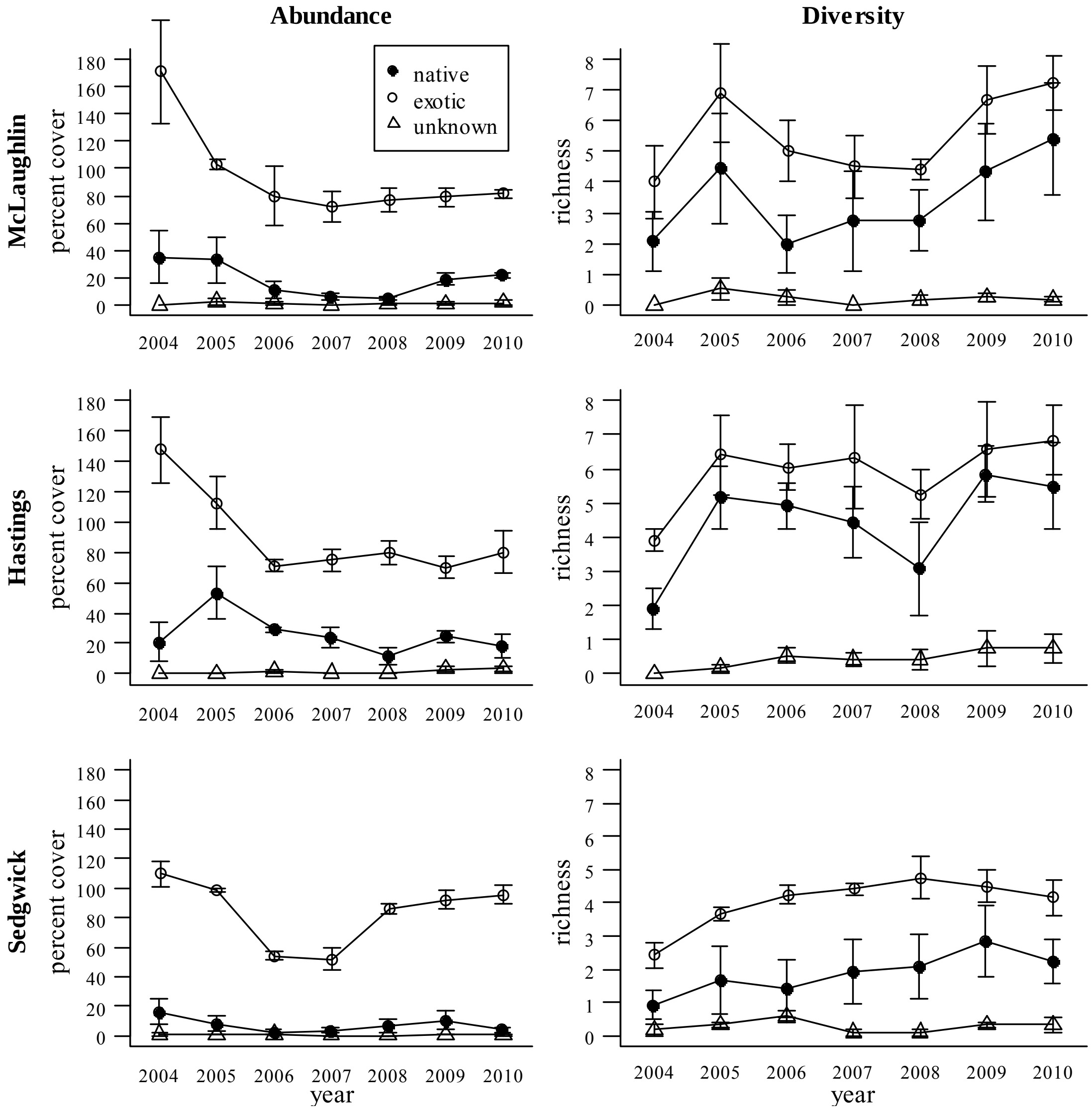


Figure 2.2: Abundance and diversity of native, exotic, and unclassifiable plants in California grassland plots at three sites (McLaughlin Natural Reserve, Hastings Natural History Reservation, and Sedgwick Reserve) sampled for 7 years. Abundance (left-hand column) was estimated as the percent areal cover; diversity (right-hand column) was the number of species observed in each group in each plot. A nested sampling design was used, with four plots within each of three blocks at each of the three sites, for a total of 36 samples in each year (*n* = 35 in 2005 and 2006 due to missing data). Responses were averaged within blocks, and values presented are means ± SE of block means; thus error bars represent within-site variability in responses.

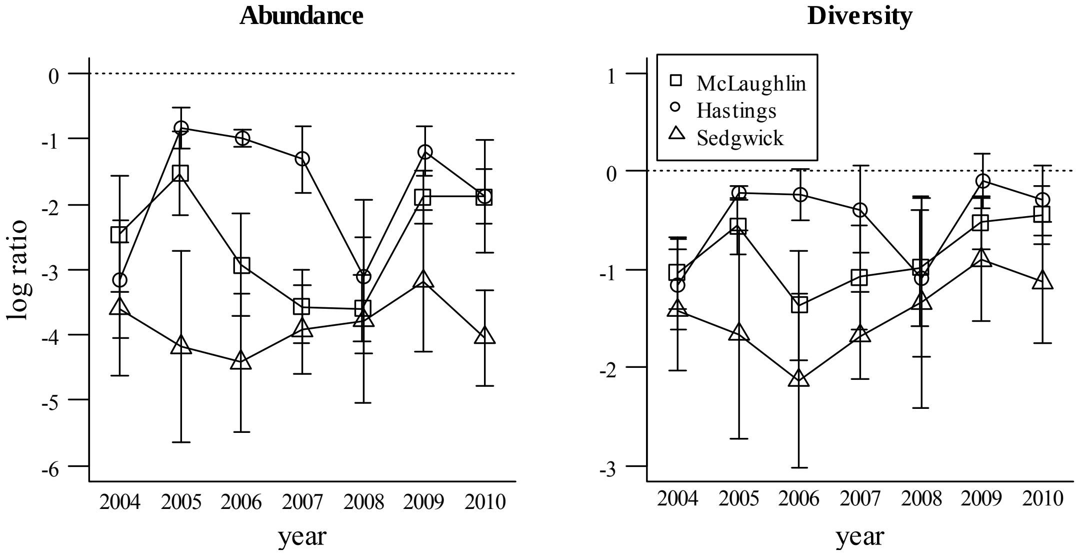
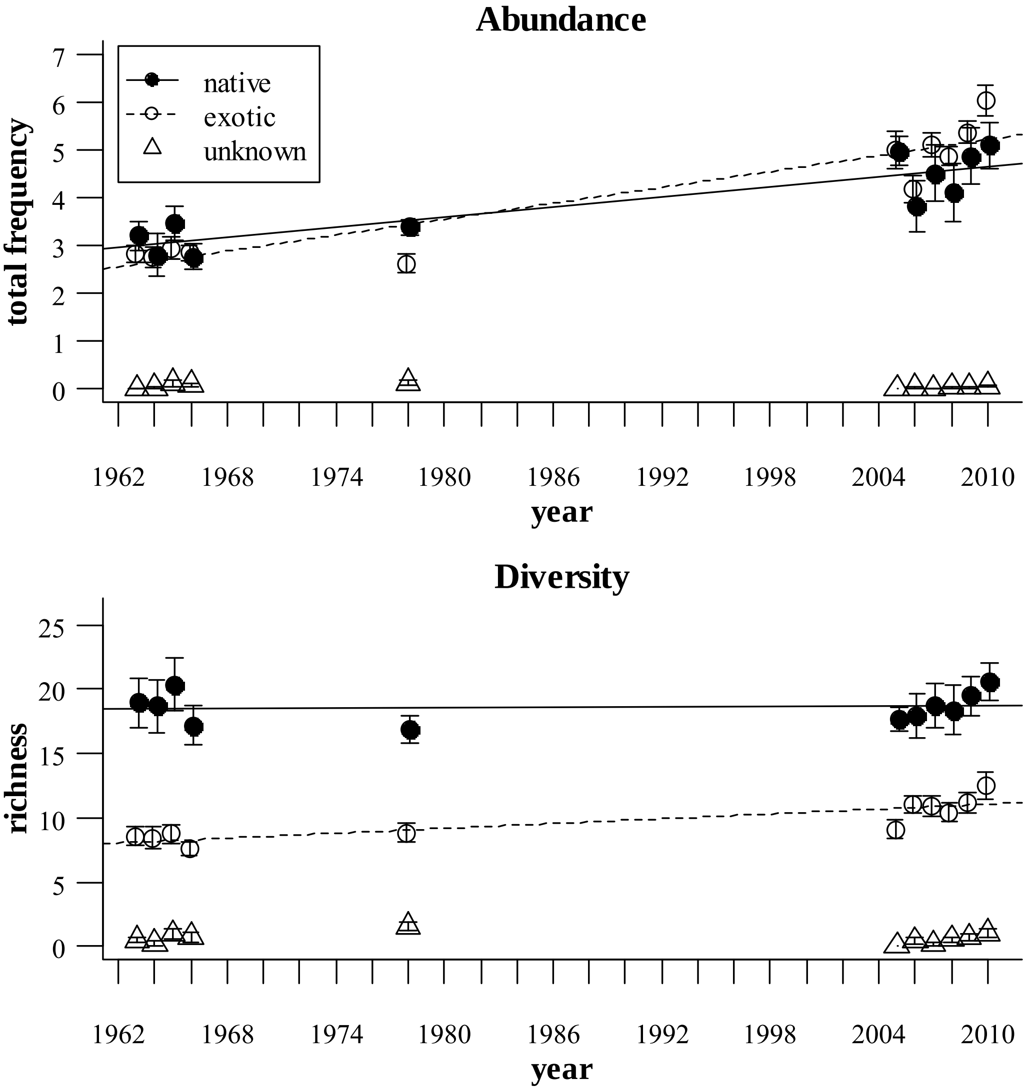


Figure 2.3: Ratios of native to exotic abundance and diversity in California grassland plots at three sites (McLaughlin Natural Reserve, Hastings Natural History Reservation, and Sedgwick Reserve) sampled for 7 years. Ratios were calculated as ln([native response + 0.1]/[exotic response + 0.1]) for each plot's native and exotic plant abundance and diversity, estimated as percent cover and richness, respectively. Negative values (below dotted lines) indicate that the native response was less than the exotic response.


Abundance

Diversity

Figure 2.4: Abundance and diversity of native, exotic, and unclassifiable plants in 11 California grassland blocks at the Hastings Natural History Reservation sampled for 11 years within a 48-year time span. Abundance was estimated as the summed frequency of native, exotic, or unclassifiable plants per block (frequency = number of quadrats in which a species was observed/total number of quadrats sampled). Diversity was estimated as the bootstrapped mean number of species observed in each group from 1000 iterations of 20 randomly selected quadrats in each block. Values presented are means ± SE; thus error bars represent within-site variability in responses. Trendlines are from a simple linear regression of each provenance group's responses over time.

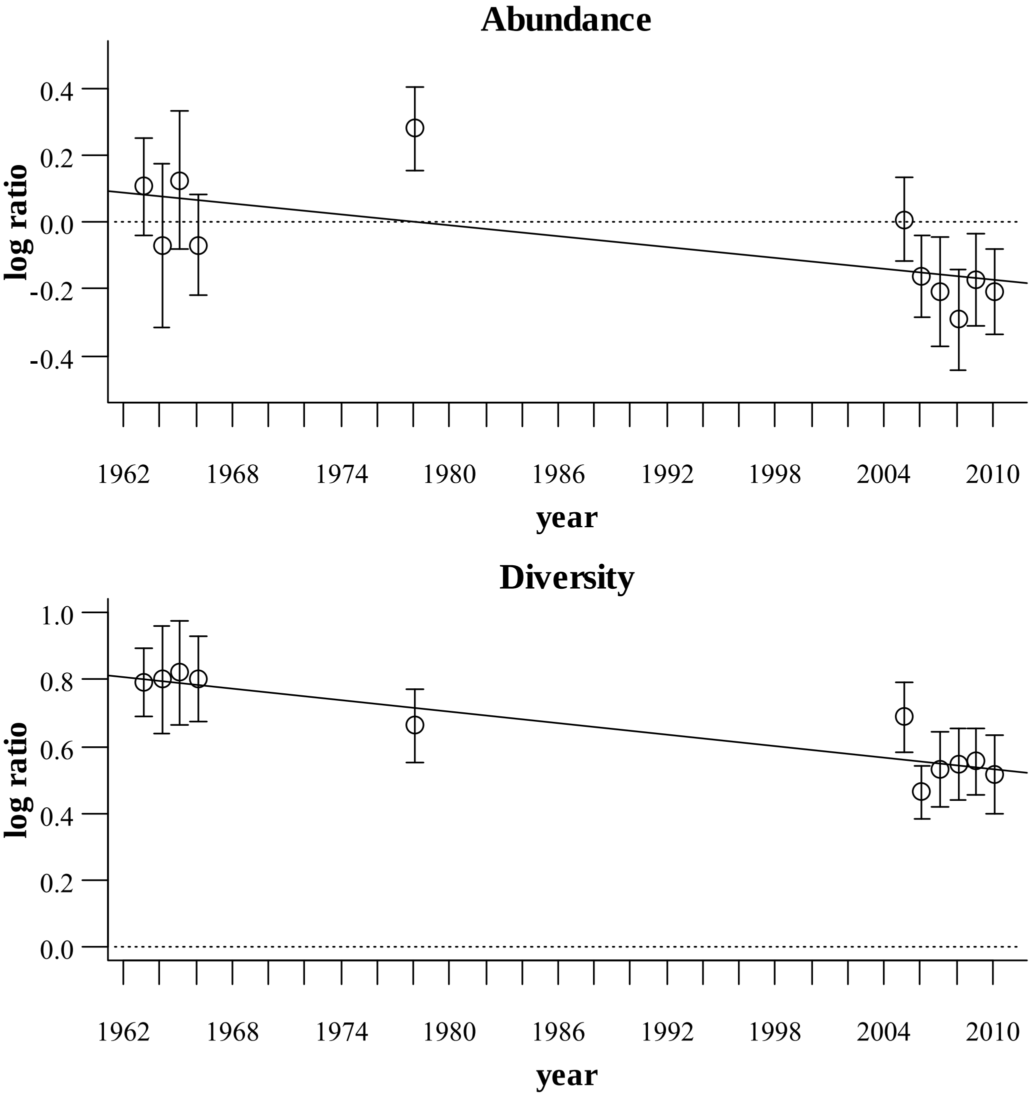


Figure 2.5: Ratios of native to exotic abundance and diversity in 11 California grassland blocks at the Hastings Natural History Reservation sampled for 11 years within a 48-year time span. Ratios were calculated as ln(native response/exotic response) for each block's native and exotic plant abundance and diversity, estimated as total frequency and richness, respectively. Negative values (below dotted lines) indicate that the native response was less than the exotic response. Trendlines are from a simple linear regression of each response over time.

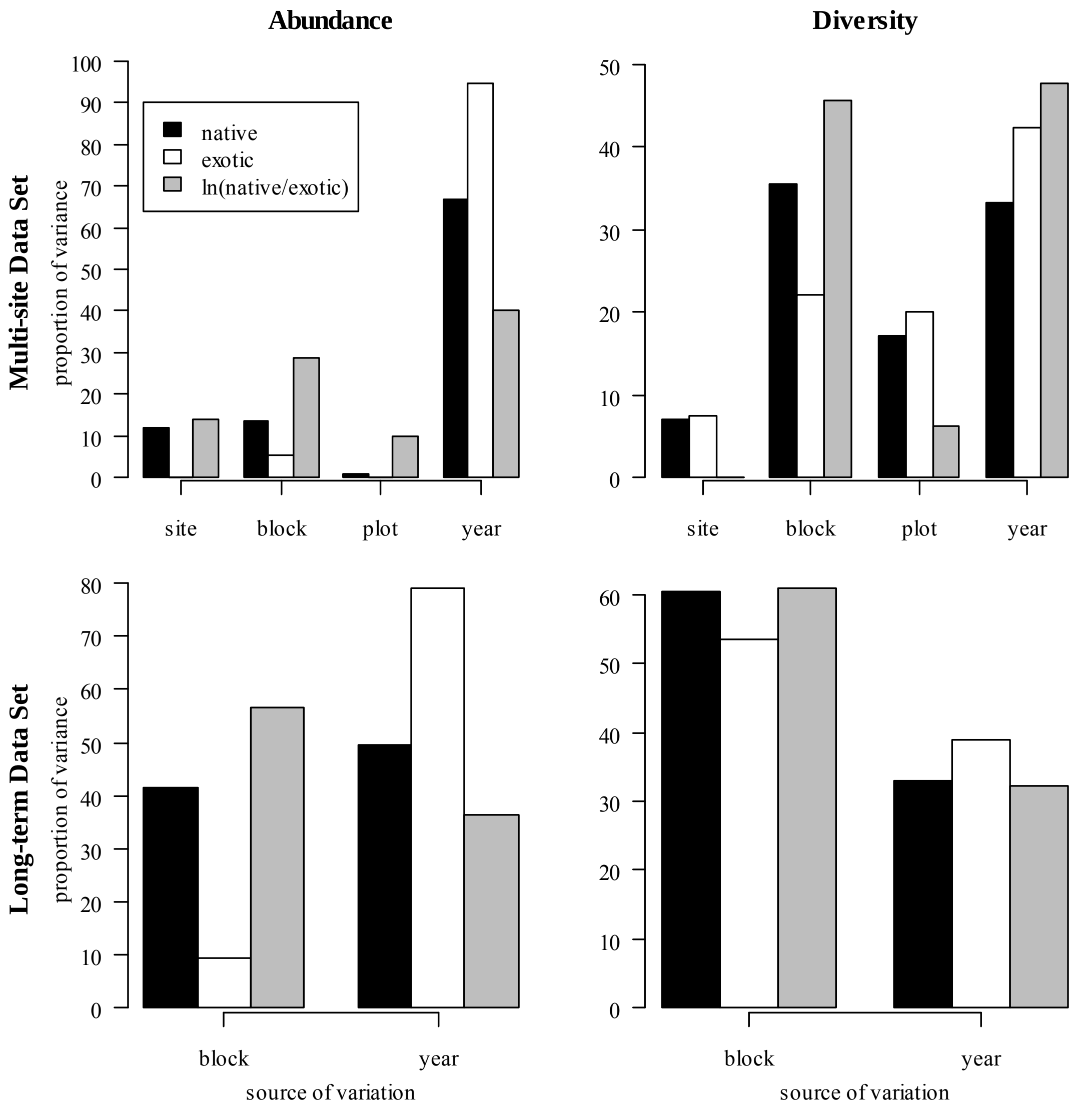


Figure 2.6: Percentage of variance in abundance and diversity of native and exotic plants and log ratios of native to exotic abundance and diversity accounted for by nested spatial and temporal variables. The top row is from a data set spanning three sites, where plots were nested within blocks within sites and were sampled for 7 years. The bottom row is from a data set spanning 48 years within one site, where blocks were sampled for 11 years within that time span.

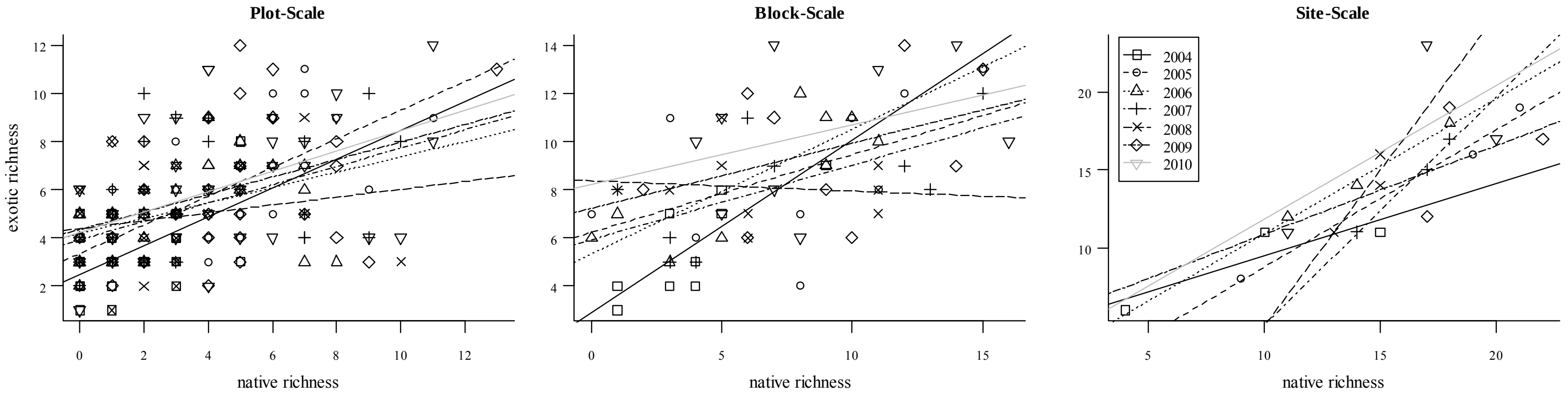


Figure 2.7: Exotic vs. native species diversity at three spatial scales over seven years. A nested sampling design was used, with four plots within each of three blocks at each of three sites, and diversity was estimated as native and exotic species richness at each scale. The native–exotic diversity relationship was generally positive at all scales, with an interaction effect for the 2008 data at the block scale (see Table 2.2).

3 – Seed- and establishment-limitation contribute to long-term declines of native forbs in California grassland metacommunities

Angela J. Brandt and Eric W. Seabloom

ABSTRACT

The effects of exotic species invasions on biodiversity vary with spatial scale, thus using community assembly theory can inform both our understanding of exotic impacts on native species at local scales and regional-scale management efforts to promote native persistence. Plant recruitment is a key factor in population and metapopulation persistence. Recruitment is limited by a combination of propagule-limitation and establishment-limitation processes. We used long-term (48 year) observational data and field experimentation to quantify propagule- and establishment-limitation in a suite of native annual forbs in California. We added seed of six native annual forbs into 22 sites that had differed in long-term population trends and grazing history and plots with experimental manipulations of plant litter and live grass competition removal. Exotic annual plants have continued to increase in abundance over the past 48 years, suggesting the system has not reached equilibrium more than 250 years after exotic species began to spread and 70 years after livestock grazing ceased. Focal species went extinct from more local populations than were colonized over the course of monitoring as a result of both propagule- and establishment-limitation. Recruitment was highest at sites that had current or historical occurrences of the seeded species and in plots where litter was removed. Grazing history (i.e., location within or outside the reserve) and community composition also influenced effects of competition removal treatments on recruitment. Thus, propagule-limitation, site quality, and land-use history may play important roles in plant recruitment and

local declines in invaded ecosystems, and must be considered during restoration planning in addition to exotic competition.

3.1 INTRODUCTION

Biological invasions pose one of the greatest threats to global biodiversity and significant economic resources are spent to control exotic species each year (Stein et al. 2000, Mace et al. 2005, Pimentel et al. 2005). The effects of invasions on biodiversity vary with spatial scale, however, such that regional diversity may increase following exotic species invasions due to fewer species extinctions than naturalizations (Sax et al. 2002, Davis 2003). Species extinction vs. naturalization rates at very fine scales remain somewhat uncertain, however, as both positive and negative relationships between native and exotic diversity at local scales have been observed (Sax et al. 2002, Fridley et al. 2007) and long-term data are necessary to document local extinctions. Determining the mechanisms responsible for local declines or extinctions in native species has implications for biodiversity conservation and ecological theory regarding community assembly, invasion ecology, and restoration ecology (Seabloom et al. 2003a, Seabloom et al. 2003b, Young et al. 2005). For example, maintenance of local populations is often critical to species persistence because greater population size and number reduces the probability of species extinction due to stochastic processes (Hanski et al. 1996). Population persistence within a community is determined by the processes governing community assembly—a combination of dispersal, abiotic conditions, and biotic interactions that lead to membership or exclusion of species from the community (Turnbull et al. 2000, Young et al. 2005). Records of long-term trends in local populations provide a unique opportunity to evaluate the role of various processes that limit recruitment into the community because the species' capacity to inhabit sites when all processes are acting together is known. Furthermore, temporal trends in native abundance following invasion is important in the face of "extinction debt" and "invasion debt", where the full impact of exotic species on natives may not occur for generations after the initial invasion due to the timescale of processes leading to native extinction and the speed of invaders' spread to their potential distribution, respectively (Davis 2003, Seabloom et al. 2006, Kuussaari et al. 2009).

Processes limiting plant or animal recruitment, and thus population size and persistence, are generally divided into "propagule-limitation" and "establishment-limitation". Propagule-limitation occurs due to insufficient propagule production and dispersal, while establishment-limitation occurs when abiotic and biotic conditions at a site are unsuitable for recruitment (Clark et al. 2007). A combination of propagule- and establishment-limitation processes likely contributes to recruitment limitation in local populations, and their roles can be determined through empirical manipulation in seed addition studies (Turnbull et al. 2000, Clark et al. 2007). Many plants are propagule-, or seed-, limited, though seed addition tends to result in small increases in recruitment (Turnbull et al. 2000, Clark et al. 2007). Exotic invasion can change environmental conditions, such as through novel biotic interactions or changes in ecosystem processes (D'Antonio and Vitousek 1992, Mitchell et al. 2006), and may thus alter the role of establishment-limitation mechanisms on native species recruitment. However, negative correlations often observed between native and exotic diversity (Fridley et al. 2007) are not necessarily caused by negative impacts of exotics, especially given a lack of evidence for extinctions caused solely by competition (Sax et al. 2002, Davis 2003, Seabloom et al. 2003b). Determining the roles of multiple factors limiting native recruitment in invaded systems can thus apply community assembly theory to inform conservation efforts.

The California grasslands provide a useful model system to explore mechanisms limiting recruitment of native species in invaded ecosystems as past work has demonstrated a role for many of these mechanisms. Eurasian annual grasses and forbs began to invade in the mid-1700s and have dominated the grasslands since at least the mid-1800s (Heady 1977, Hamilton 1997a, Mensing and Byrne 1998). Though few native plant extinctions have been documented relative to the high floral diversity in California (Stein et al. 2000, California Native Plant Society (CNPS) 2011), natives remain limited in regional abundance and are often locally restricted to habitat refugia or sites with certain land-use history (Stromberg and Griffin 1996, Seabloom et al. 2003a). Seed limitation has often been proposed as a general explanation for these patterns (Seabloom et al. 2003a, Seabloom et al. 2003b; but see Moore 2009). High spatial heterogeneity in the abiotic environment may limit the suitable sites for a species within its geographic range (Sax and Brown 2000, Moore 2009). Anthropogenic disturbances and the consumer community appear to have varied effects on plant recruitment, potentially decades after land-use change (Stromberg and Griffin 1996, Hayes and Holl 2003a, b, Orrock et al. 2008, 2009, Seabloom et al. 2009). Livestock grazing effects may vary among sites and species due to direct effects (e.g., via seed limitation caused by herbivory) or indirect effects (e.g., via altering plant community composition and biomass) (Hayes and Holl 2003a, b, Orrock et al. 2008). Finally, as few annual grasses are native to the system, the exotic community represents a suite of novel plants that may have altered the competitive environment for native seedlings in two primary ways. Early germination and rapid shoot growth of annual grasses in the fall may increase limitation of light and moisture resources for native seedlings (Dyer and Rice 1999, Coleman and Levine 2007). Substantial build-up of plant litter can occur in annual grass-dominated communities, inhibiting native seed germination and establishment (D'Antonio and Vitousek 1992, Foster and Gross 1998, Coleman and Levine 2007). Modeling work has also demonstrated that rare native forb persistence can be impacted by annual grass litter that inhibits germination (Levine and Rees 2004). Distinguishing the roles of these different mechanisms of exotic annual grass competition with native seedlings would therefore inform both existing theory about biotic interactions within the system and effective management strategies for promoting native recruitment.

Recruitment-limitation in California grasslands can be explored within the context of local community trends via seed addition studies. Recruitment within this annual-dominated system depends heavily on early life stages given the dominance of annual species and following plants for one year provides documentation of recruitment to adulthood. Additionally, we can relate these mechanisms to long-term patterns in local communities using monitoring data from the Hastings Natural History Reservation (HNHR) in central California. Native and exotic plant diversity in local communities within HNHR were relatively stable from 1963-2010, however exotics are becoming increasingly dominant (Brandt and Seabloom In press). Furthermore, long-term local population trends were idiosyncratic, regardless of provenance (native or exotic), life history, or functional group (grass or forb) (A. J. Brandt, *unpublished data*). These local grassland communities may therefore be continuing to undergo changes in recruitment dynamics even a century after exotic dominance and decades after livestock grazing ceased.

Our objectives were to determine whether California grassland communities at fine spatial scales exhibited stable long-term patterns and which processes limit recruitment of native species into these invaded communities. We used paired monitoring transects inside and outside the boundary of a natural reserve to examine local community and population patterns approximately 100-150 years following the main invasion of the system and approximately 25-75 years after cattle grazing ceased inside the reserve. To determine the roles of seed limitation, habitat suitability, and biotic interactions in limiting native species recruitment, we added seed of six native annual forbs to experimental plots adjacent to these monitoring transects where exotic annual grass competition via the growth of grass seedlings and build-up of plant litter was removed in a factorial design. Though an important component of biodiversity in California grasslands, native forbs remain under-studied compared to grasses due to debate about the true historical composition of the system (Hamilton 1997a, Seabloom et al. 2003a). Nesting experimental plots within the framework of the long-term study allowed us to make the following predictions: 1) if seeded species recruit across sites and treatments, then seed limitation drives local abundance; 2) if seeded species recruitment is greater in sites occupied by those species during monitoring, then habitat suitability drives local abundance; 3) if seeded species recruitment is greater in competition removal plots, then exotic annual grass competition drives local abundance; and 4) if seeded species recruitment differs inside vs. outside the reserve, then the history of consumers drives local abundance. We tested for interactive effects of these processes because, for example, the effects of litter removal may depend on grazing history.

3.2 METHODS

Work was conducted at the Hastings Natural History Reservation (HNHR), Monterey County, California, USA (36º22´N, 121º32´W), a 1000-ha reserve established in 1937 as part of the University of California’s Natural Reserve System.

A grazing-effects study was established in 1963 and sampled from 1963-66, 1978, and 2005-2010. The sampling design consisted of 11 pairs of transects along the reserve boundary, one inside and one outside of the reserve, in a range of open canopy to oak woodland habitats to monitor understory plant community composition. In 1963, cattle grazing occurred at all sites outside the reserve boundary. Since 1963, the reserve acquired two sites and cattle grazing ceased on others, thus only three sites were still grazed in 2005-2010. Presence of each species was recorded in 20 to 120 20×50-cm quadrats regularly spaced throughout each site during peak biomass (April-June) (Brandt and Seabloom In press). Permanent 40-m transects were marked at each site in 2006. Abundance of all annual plant species within transects was estimated for provenance (native and exotic) and functional groups (grass and forb) by summing frequency of species in each group, where frequency is the number of quadrats in which a species was observed divided by the total number of quadrats sampled per transect. Abundance of six native annual forb species (*Castilleja exserta* (Scrophulariaceae), *Clarkia purpurea* (Onagraceae), *Collinsia heterophylla* (Scrophulariaceae), *Nemophila menziesii* (Hydrophyllaceae), *Plantago erecta* (Plantaginaceae), and *Trifolium microcephalum* (Fabaceae)) was estimated as frequency per transect. A factor variable was created for each transect to describe the long-term occupancy trend for each species. “Stable occupancy” was defined as documented presence of a species during both the early (1963-1978) and late (2005-2010) monitoring periods. “Extinction” was defined as documentation of a species’ presence only during the early monitoring period, and “colonization” was defined as documentation of presence only during the late monitoring period (Table 3.1).

A seed addition experiment was nested within the long-term monitoring design to determine the relative role of several factors in limiting species recruitment. The same six native annual forbs were seeded into competition removal plots located adjacent to monitoring transects in a two-way factorial design in September 2009 (see *Appendix D* for a figure of the design). A block of four 1 × 1.5 m treatment plots was placed at the ends and middle of each transect on each side of the reserve boundary, for a total of 264 plots. Each species was seeded into one of six regularly spaced locations within a 0.5 × 1 m cover quadrat and marked with a plastic cocktail sword, such that each species was sown a minimum distance of 30 cm from other seeded species. Seeding location for each species was randomly assigned for each plot. Species with laboratory trial germination rates >25% (*Clarkia* and *Collinsia*) were seeded at a rate of 30 seeds per plot, while the other four species were seeded at a rate of 40 seeds per plot. Species were chosen based on preliminary observations of presence and population declines within multiple monitoring transects and availability of seed for the experiment. Seed was purchased from native seed suppliers in California (Larner Seeds, Pacific Coast Seed, Inc., and Rana Creek); only *Castilleja* seed had been wild-collected local to HNHR. Competition removal treatments were randomly assigned to plots within blocks, applied in a factorial design, and consisted of removing plant litter via hand clipping or removing live grass via herbicide. Litter was removed when plots were established, dried to constant mass, and weighed. Grass-specific herbicide (sethoxydim, with N-90 non-ionic surfactant) at a concentration of 8 ml per L water was applied at a rate of 0.1 L per plot following initial germination of annual grasses in October-November 2009 and again in late December 2009. During herbicide application, seed-sowing locations within plots were covered with plastic containers and then grass underneath these containers was brushed with herbicide. Numbers of individuals of each seeded species at the seed-sowing locations were counted in March and May 2010. Community composition was visually estimated as percent cover of all grasses and forbs within each cover quadrat in October-November 2009, December 2009, and March 2010, and as percent cover of individual species in May 2010. All statistical analyses were conducted in in R 2.11.1 (R Development Core Team 2010) and mixed-effects models used the nlme R library (Pinheiro et al. 2010) or the lme4 R library for models with Poisson errors (Bates and Maechler 2010).

3.2.1 Analyses of Long-term Monitoring Trends

The effects of time, land-use history (i.e., location inside or outside the reserve), native status (i.e., native or exotic), and functional group (i.e., grass or forb) on total frequency of annual plants in long-term monitoring transects were determined with mixed effects models. The sampling design was incorporated into each model as nested random effects, with year nested within the two transects (inside or outside reserve) and transect nested within site. The full model included a four-way interaction between all predictors. Models were estimated using maximum likelihood and model simplification was performed using ANOVA to find the model with the lowest AIC.

The effects of time, land-use history, and species on frequency of the six native annual forb species of interest in long-term monitoring transects were determined with mixed effects models. The sampling design was incorporated into each model as nested random effects, with year nested within the two transects (inside or outside reserve) and transect nested within site. The full model included a three-way interaction between all predictors and was estimated using restricted maximum likelihood.

3.2.2 Analyses of Focal Species Recruitment

The effects of competition removal treatments, land-use history, long-term occupancy trends at a transect, the mean mass of litter removed from a block, and plant community composition within a plot on both total recruitment of seeded forb species and recruitment of individual species were determined with mixed effects models with Poisson errors because responses were counts. The experimental design was incorporated into each model as nested random effects, with sampling date nested within block, block nested within the two transects (inside or outside reserve), and transect nested within site. Full models included a three-way interaction between land-use history and competition removal treatments. Orthogonal contrasts of long-term occupancy trends for models of individual species responses were used to compare 1) sites with at least a single documentation of presence vs. sites where a species was never observed, 2) sites where a species had gone extinct vs. sites with documented presence during the late monitoring period, and 3) sites with stable occupancy vs. newly colonized sites. Models were estimated using maximum likelihood and model simplification was performed based on AIC.

The effects of competition removal treatments, land-use history (i.e., location inside or outside the reserve), functional group (i.e., grass or forb), and sampling date (i.e., fall, winter, early spring, or late spring) on percent cover of vegetation were determined with mixed effects models. The experimental design was incorporated into each model as nested random effects, with sampling date nested within plot, plot nested within block, block nested within the two transects (inside or outside reserve), and transect nested within site. The full model included three-way interactions between competition removal treatments and each of the other predictors, and all two-way interactions between land-use history, functional group, and sampling date. Orthogonal contrasts for sampling date were used to compare responses 1) before and after the initial herbicide application (i.e., fall vs. other sampling dates), 2) before and after the second herbicide application (i.e. winter vs. both spring sampling dates), and 3) early vs. late spring. Model simplification was based on AIC.

3.3 RESULTS

3.3.1 Long-term Monitoring Trends

Total frequency of annual plant groups has generally increased in monitoring transects over the past 48 years ($P < 0.0001$; Fig. 3.1), however trends differed by plant group and land-use history (i.e., location inside vs. outside the reserve boundary). Exotic plant total frequency increased more over time than native frequency, especially due to the temporal stability of the single native annual grass species, *Vulpia microstachys* ($P = 0.03$ for the interaction between year and native status, and $P = 0.0001$ for the interaction between year, native status, and functional group). Total frequencies of plant groups increased more inside the reserve boundary than outside of it, especially for native forbs ($P = 0.05$ for the interaction between year and land-use history, $P = 0.09$ for the interaction between year, land-use history, and native status, and $P = 0.01$ for the interaction between year, land-use history, and functional group).

Temporal trends in site occupancy (Table 3.1) and frequency within occupied sites differed among native annual forb species (Fig. 3.2; see *Appendix E* for predictor effect sizes and significance). The six focal species were generally observed in many of the long-term monitoring transects at some point during both the early and late monitoring periods (Table 3.1). However, observed extinctions from transects were more common than colonizations of new transects. General declines in frequency over time were observed for *Castilleja* ($P = 0.04$) and *Plantago* ($P = 0.03$), while general increases were observed for *Clarkia* ($P = 0.009$) and *Trifolium* ($P = 0.008$). Mean frequency and temporal frequency trends also differed by land-use history for certain species. Lower mean frequencies were observed in transects inside the reserve boundary for *Castilleja* (*P* = 0.08) and outside the reserve boundary for *Collinsia* (*P* = 0.009), while land-use history did not affect mean frequency of the other species (*P* > 0.7). Declines in *Castilleja* frequency occurred primarily in transects outside the reserve boundary (*P* = 0.05 for the interaction between year and land-use history), and *Collinsia* exhibited stronger increases inside the reserve boundary (*P* = 0.001 for the interaction between year and land-use history). Land-use history did not affect temporal trends in frequency of the other species (*P* > 0.7)

3.3.2 Focal Species Recruitment

Multiple predictors affected recruitment of the seeded plants and recruitment of each species was often differentially affected by these predictors (see *Appendix F* for predictor effect sizes and significance in final mixed effects models). Species recruitment was low overall (6.2% of total seeds sown), with 1.2% recruitment of *Castilleja*, 6.7% recruitment of *Clarkia*, 7.4% recruitment of *Collinsia*, 5.1% recruitment of *Nemophila*, 11.4% recruitment of *Plantago*, and 6.2% recruitment of *Trifolium*. However, recruitment occurred at all sites for five of the six seeded species. *Castilleja* did not recruit in four of the 22 transects, which were located at three sites, both inside and outside the reserve boundary, where populations were either never documented or went extinct according to monitoring data. Long-term occupancy trends along a transect were good predictors of species recruitment for *Castilleja* (*P* = 0.04 for increased recruitment in transects it had occupied compared to transects in which it was never documented), *Collinsia* (*P* = 0.02 for increased recruitment in transects it had occupied compared to transects in which it was never documented), *Nemophila* (*P* < 0.0001 for increased recruitment in transects with stable occupancy compared to colonized transects), and *Plantago* (*P* = 0.02 for increased recruitment in transects it had occupied compared to transects in which it was never documented) (Fig. 3.3). However, mean observed frequency of a species in a transect over the course of monitoring was never a good predictor of recruitment (see *Appendix F*).

Competition removal treatments and the plant community also affected seeded species recruitment, though land-use history tended to alter recruitment responses to experimental treatments (see Fig. 3.4 for total recruitment response and *Appendix G* for species-specific responses). Total recruitment was generally greater when litter was removed (*P* = 0.002). However, the effects of herbicide application were complex, with increased recruitment in plots outside the reserve where litter was not removed and the strongest decreased recruitment in plots inside the reserve where litter was not removed (*P* < 0.0001 for the interaction between litter and herbicide treatments, *P* = 0.02 for the interaction between herbicide treatment and land-use history, and *P* = 0.0001 for the three-way interaction between herbicide treatment, litter treatment, and land-use history). The positive effect of litter removal was stronger for plots inside the reserve boundary (*P* = 0.003 for the interaction between litter treatment and land-use history). Total recruitment increased with total forb cover (*P* < 0.0001), but decreased with increasing cover of exotic forbs (*P* = 0.01).

Recruitment also decreased as the mass of litter removed from experimental plots increased (*P* = 0.02). Competition removal treatments, especially herbicide application, significantly reduced grass cover and increased forb cover (see *Appendix H*). Grass cover was generally greater in plots located inside the reserve boundary and forb cover was greater outside the reserve (*P* = 0.001 for the interaction between functional group and land-use history). In particular, exotic forb cover during the spring samplings was greater outside the reserve (*P* = 0.02) and application of herbicide increased exotic forb cover overall (*P* < 0.0001), thus the highest cover of exotic forbs was observed in plots outside the reserve boundary where herbicide was applied (*P* = 0.003 for the interaction between herbicide application and land-use history). Mean mass of litter removed from each experimental block in fall 2009 did not differ across the reserve boundary (*P* = 0.7 from mixed effects model including nested random effects of block within side of boundary within site), but annual grass cover at a site in the spring was correlated with mean mass of litter removed from that site in the fall (*r* = 0.65, *P* = 0.001).

3.4 DISCUSSION

California grassland communities appear to be exhibiting long-term transience centuries after exotic plant invasion and decades after livestock grazing ceased. Abundances of annual plant groups and six native annual forbs demonstrate that the system is continuing to change (Fig. 3.1 and 3.2, Table 3.1). A combination of seed-limitation and establishment-limitation processes appear to be impacting recruitment of these native annual forbs, which likely explains observed population declines (Fig. 3.3 and 3.4).

The long-term transience in grassland community dynamics suggested by our data indicate that exotic invaders are continuing to impact native species. We observed high interannual variability in community composition, which is common in California grassland communities, especially given the region’s temporal variability in climatic conditions (Pitt and Heady 1978, Michaelsen et al. 1987, Brandt and Seabloom in press). However, long-term trajectories of increasing exotic abundances within transects seen here suggest that an “invasion debt” remains to be paid even within sites where certain exotic species have been present for a century (Seabloom et al. 2006). The effects of exotic invaders on the system, including their role in limiting native species recruitment, may therefore continue to increase. The greater number of population extinctions than colonizations that we observed over the past 48 years for certain native forbs suggests they may eventually be extirpated from the reserve without management intervention. According to metapopulation theory, decreases in the number of local populations increases overall risk of complete extirpation from areas of each species’ range due to stochastic events, as well as lowered opportunities for immigration from neighboring populations (Hanski et al. 1996). Further demographic work and more extensive surveys of these species’ populations are necessary to confirm our findings, however. Continued population monitoring, including long-term responses to management actions, would aid conservation of these species.

Recruitment of these six native forbs was generally low, as is typical of seed limitation generally (Clark et al. 2007), but our observations of recruitment across all sites suggest that populations are seed-limited. Seed-limitation is common for plants, especially annuals (Turnbull et al. 2000, Clark et al. 2007), has been documented for many species in California grasslands (Seabloom et al. 2003a, Seabloom et al. 2003b), and is likely to be exacerbated by other factors causing population declines, such as anthropogenic disturbance and biological invasions. Viable seed banks may reduce seed-limitation, however, and many native California forbs exhibit seed dormancy (e.g., Levine and Rees 2004, Moore 2009). Seed addition may still be necessary to restore many native populations, as disturbance to remove exotic competition does not always increase native recruitment or richness (Hayes and Holl 2003b, Seabloom et al. 2003a, Coleman and Levine 2007).

Documented species occupancy and abundance for specific sites can provide valuable insight into the suitability of those sites for species restoration. Identifying and measuring all important habitat attributes for a species is rarely feasible, and suitable habitat is likely to be patchily distributed given the varying scales of spatial heterogeneity in abiotic and biotic environmental gradients (Sax and Brown 2000, Moore 2009). Here, recruitment was higher at sites with historical or current occupancy, suggesting that restoration focused on sites known to be suitable (i.e., population augmentations) may be more effective than attempting restoration on other apparently similar sites (i.e., population introductions). Overall population abundance was a poor predictor of recruitment, perhaps because community observations demonstrate the ultimate result of all processes acting on recruitment. However, temporal trends in species abundances provided reasonable predictions of negative impacts of exotic species on native populations. *Collinsia* and *Trifolium* populations generally increased, and their recruitment did not appear limited by exotic grass competition (see *Appendices F* and *G*). However, similar long-term abundance patterns may not be generated by the same mechanisms of recruitment-limitation. Site suitability (i.e., documented population at a site) also enhanced *Collinsia* recruitment and, though *Clarkia* populations increased in abundance, competition removal increased recruitment. Long-term monitoring records can thus help identify suitable habitat that is currently unoccupied, which is important to maintaining a viable metapopulation (Hanski et al. 1996), but determining which mechanisms limit establishment of species with declining local populations may still be necessary to promote population persistence.

Competition from exotic species likely plays a complex role in recruitment-limitation of native forbs and may continue to increase in impact as exotic invaders are predicted to continue expanding in range and abundance (Seabloom et al. 2006). Here, competitive effects of exotic annual grasses were largely indirect, being mediated by plant litter (but see Coleman and Levine 2007). Native California forbs have little evolutionary history with annual grasses and associated accumulations of litter. This result supports previous modeling results where litter build-up is a key component influencing germination and recruitment of native forbs into the system (Levine and Rees 2004), observations of increased native annual forb richness and cover with reduced litter depth (Hayes and Holl 2003a), and increased native forb richness and cover in litter removal experiments (Coleman and Levine 2007). Thus, in systems where exotic invaders are biased toward a specific novel plant group, such as annual grasses, novel competitive mechanisms may promote establishment-limitation in native populations and management focused on mitigating these competitive effects may be most effective at restoring native species. The exotic forb community may also play an important role in regulating native forb recruitment. Recruitment of native forbs decreased with increasing exotic forb cover, which may in part explain lower recruitment in plots where grass-specific herbicide was applied and lower recruitment in plots outside the reserve boundary for certain species. Plants with similar traits can limit recruitment (Fargione et al. 2003, Moore 2009) and early season forbs may enhance competition for certain soil resources relative to grasses or late season forbs (Hooper and Vitousek 1997). Thus, exotic forbs that share traits and resource acquisition strategies may be stronger competitors with native forbs than exotic annual grass seedlings. Future work comparing effects of exotic forbs and grasses on native forb recruitment would elucidate the relative impact of different members of the invader community.

Livestock grazing alters community composition, and thus can both directly and indirectly influence recruitment. Our results suggest that grazing can produce a legacy effect, such that differences in community composition and recruitment-limitation processes may persist for decades following cessation of grazing. Though we observed some species-specific responses to grazing history, native forbs in general responded differently to exotic competition removal treatments based on a site's grazing history. This may be due, in part, to differences in community composition across the reserve boundary but was not due to differences in the accumulation of litter. Current grazing regimes have been shown to increase richness and cover of California annuals, including native annual forbs, in part due to decreased litter depth and vegetation height associated with grazed areas (Hayes and Holl 2003a). Here, we have decoupled the confounding effects of grazing and litter, thus demonstrating that the primary mechanism for the positive effect of cattle was likely the reduction of litter (but see Hayes and Holl 2003b). The many ecosystem effects of livestock grazing are difficult to reproduce and may be site-specific (Hayes and Holl 2003b), but examining the roles of multiple recruitment-limitation processes better elucidates our understanding of the factors that are driving population declines.

Here we have shown that recruitment-limitation processes may differentially affect species that are expected to be ecologically similar *a priori*, such as native annual forbs. Though seed-limitation and certain establishment-limitation processes were generally important, the strength and direction of the effects of site occupation, grazing history, and competitive mechanisms differed among species. Recruitment thus appears “niche-limited” for these species, with different abiotic and biotic constraints on population persistence (Moore 2009). Observed long-term trends in native forb populations also suggested differential responses to grazing history of sites and temporal variability in the environment. Provenance and functional group of a species represent only two axes along which species might share traits, and evolutionary history may further indicate relevant differences among species and affect community assembly (Cavender-Bares et al. 2009). We examined forbs from six different families, thus further work to determine if the responses we observed are more similar within than among clades would improve the predictive power of this study.

Though our work was focused at a single site over one year, intensive exploration of mechanisms governing recruitment, and thus community dynamics, at local scales is important to understanding invasion impacts and informing management (Sax et al. 2002). Our results may be broadly applicable to California grasslands as *Plantago erecta* recruitment was also primarily seed-limited at another site approximately 200 km south of HNHR (Seabloom et al. 2003a). By examining annual plants, we were able to document recruitment to adulthood, but determining whether seed addition and competition removal leads to self-sustaining populations of native forbs is an important next step (Turnbull et al. 2000). The relative roles of seed- and establishment-limitation processes may fluctuate over time when temporal heterogeneity in the abiotic and biotic environment are present (Moore 2009), though our results appear somewhat robust to environmental variation given the similar findings of other studies (Hayes and Holl 2003a, b, Coleman and Levine 2007).

In conclusion, we have demonstrated that extinction of local native plant populations is more common than establishment of new populations and recruitment tends to be higher in sites with a history of species occupancy, suggesting that maintenance of documented populations is critical to long-term species persistence (Hanski et al. 1996). Both seed- and establishment-limitation processes affect native plant recruitment, with certain mechanisms of exotic plant competition providing a general native recruitment barrier. Thus, multi-faceted restoration approaches may be most effective for native plant conservation, including mitigation of exotic interaction mechanisms that are novel to the system. Finally, our work suggests that community dynamics in predominantly annual systems may remain transient centuries after exotic invasion and decades after anthropogenic disturbance. Continued monitoring and biodiversity management is thus critical as systems may still be facing an “invasion debt” and native species an “extinction debt” (Seabloom et al. 2006, Kuussaari et al. 2009).

ACKNOWLEDGEMENTS

We thank K. L. White for providing long-term data from HNHR and M. R. Stromberg, field crews, and other HNHR staff and researchers for providing field assistance. We thank the Bradleys, K. Meehan, and the O'Briens for allowing access to field sites located on their land. S. D. Hacker provided valuable comments on the manuscript. We also thank the UC Natural Reserve System. Funding for this work provided by NSF DEB-0910043, The Nature Conservancy's Oren Pollak Memorial Research Grant for Grassland Science, and UC Integrated Hardwood Range Management Program (W. D. Koenig, M. V. Ashley, E. T. Borer, J. M. H. Knops, E. W. Seabloom, and M. R. Stromberg).

Table 3.1: Long-term occupancy trends for six native annual forb species in 11 paired monitoring transects located inside and outside of the reserve boundary. Stable occupancy was documented presence during both the early monitoring period (1963-1978) and the late monitoring period (2005-2010). Species documented only during the early monitoring period were considered to have gone extinct from the transect and species documented only during the late monitoring period were considered to have colonized the transect.

Species	Number of transects inside reserve boundary				Number of transects outside reserve boundary			
	Stable occupancy	Extinction	Colonization	Never documented	Stable occupancy	Extinction	Colonization	Never documented
Castilleja exserta	3	4	0	4	2	5	0	4
Clarkia purpurea	8	2	1	0	10	1	0	0
Collinsia heterophylla	5	0	0	6	5	0	0	6
Nemophila menziesii	2	2	0	7	2	1	2	6
Plantago erecta	1	3	0	7	1	5	0	5
Trifolium microcephalum	10	0	0	1	10	0	0	1

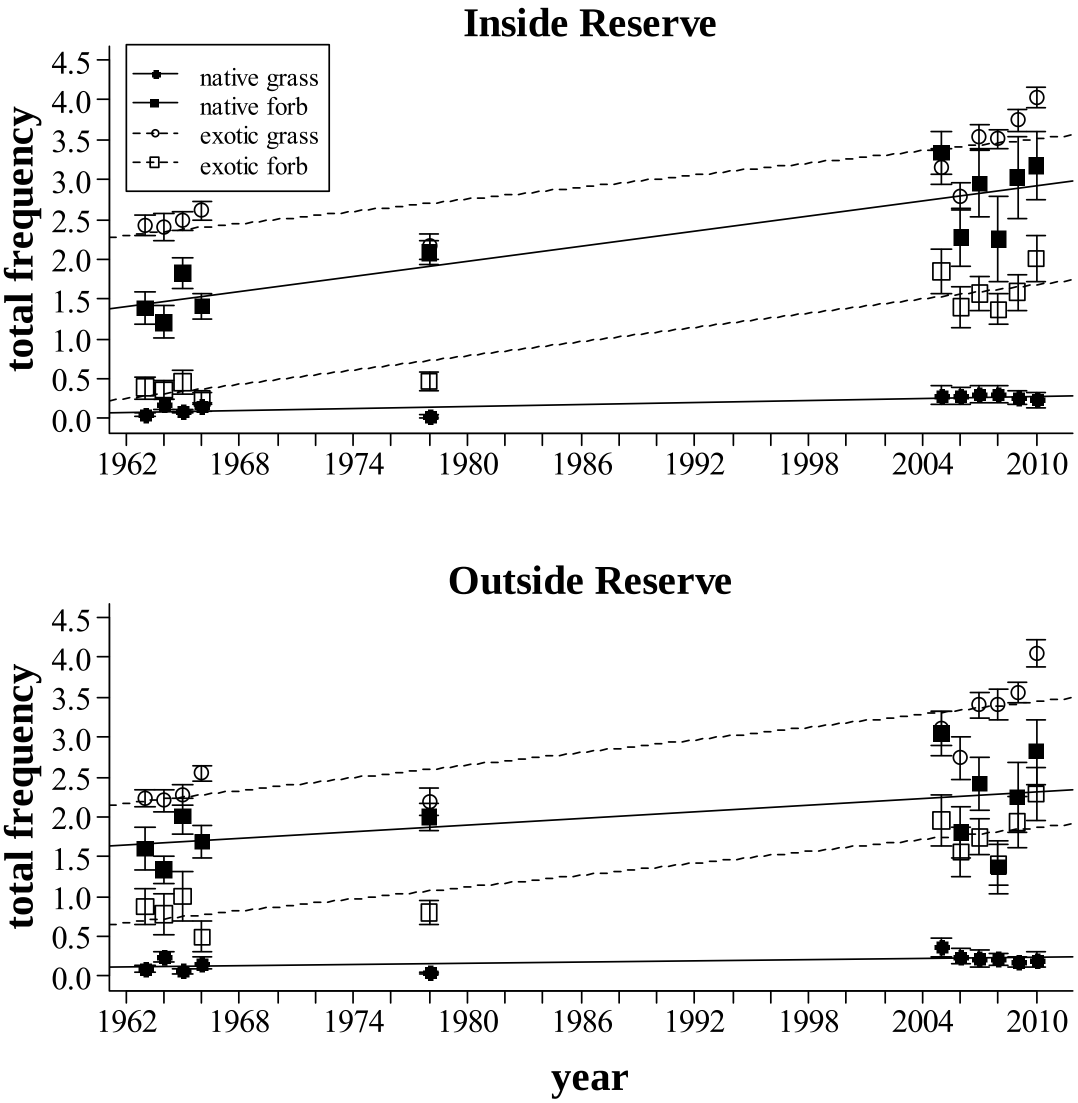


Figure 3.1: Abundance (± SE) of annual plants along 11 paired monitoring transects located inside and outside the reserve boundary. Abundance was estimated as the summed frequency of native and exotic grasses and forbs along each transect, where frequency was the number of quadrats in which a species was observed divided by the total number of quadrats sampled.

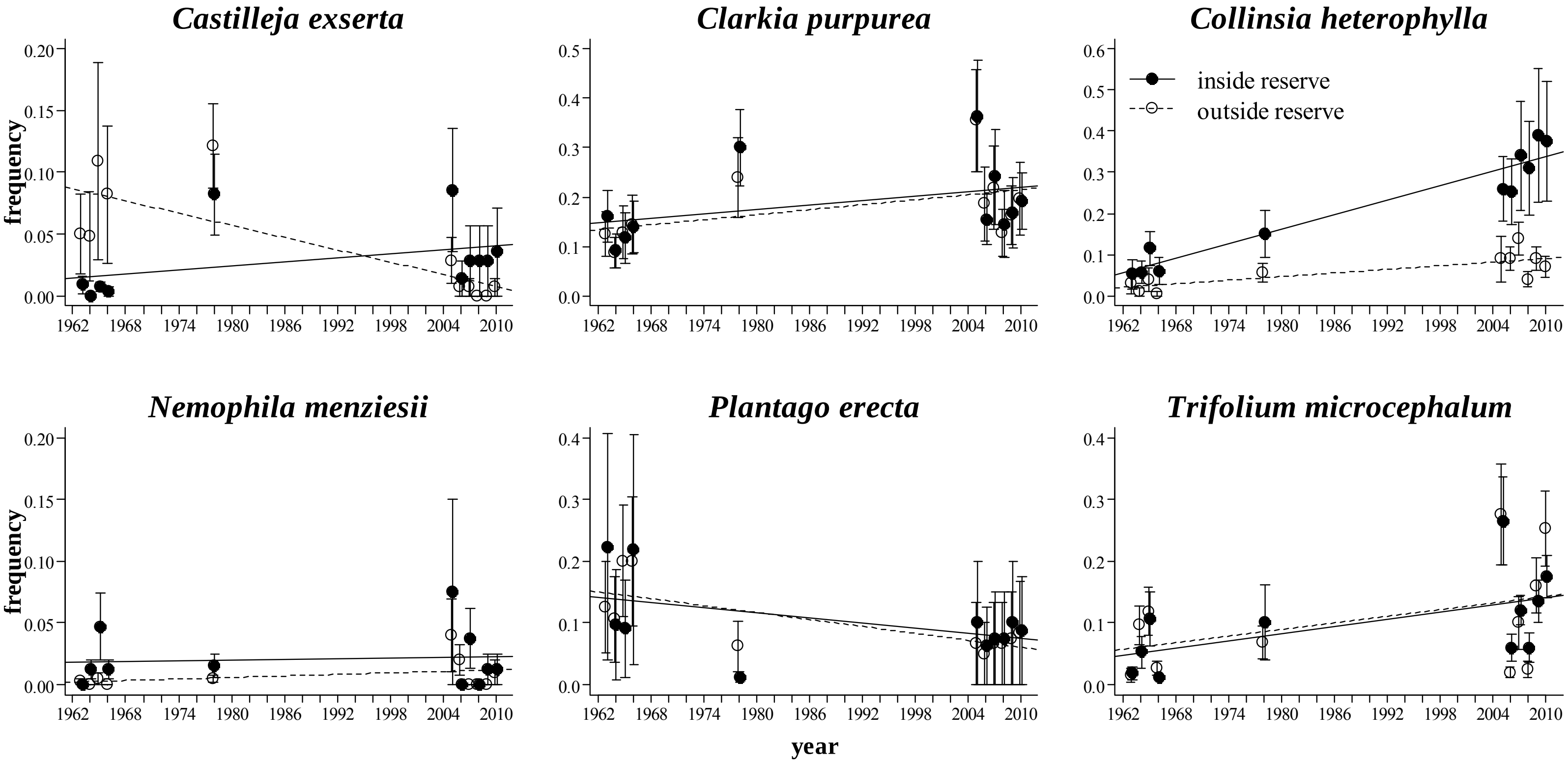


Figure 3.2: Abundance (± SE) of six native annual forbs along 11 paired monitoring transects located inside and outside the reserve boundary. Abundance was estimated as frequency of observation, or the number of quadrats in which a species was observed divided by the total number of quadrats sampled. Mean yearly abundances were calculated using only transects in which the species was observed in at least one year over the course of monitoring (see Table 3.1 for sample sizes).

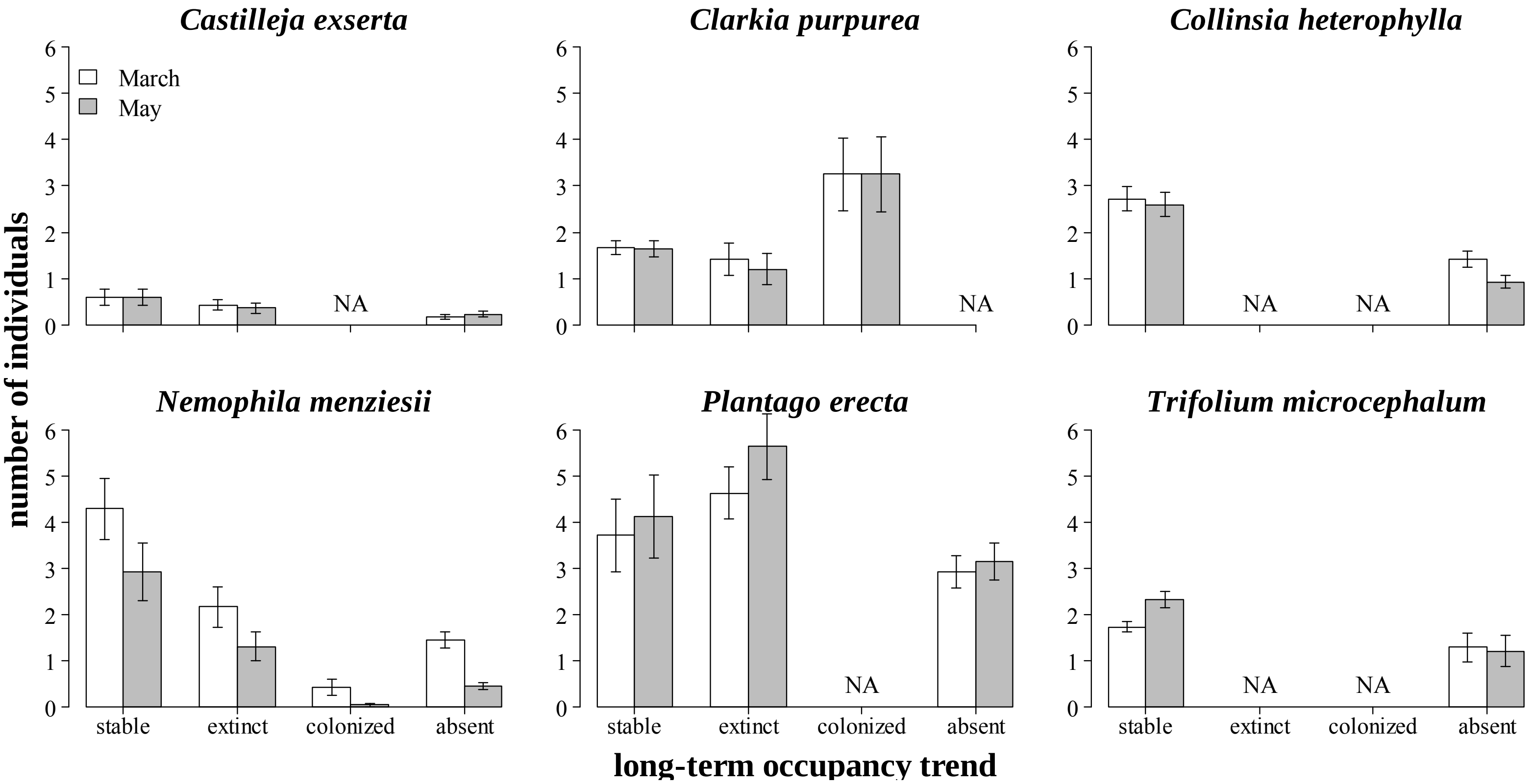


Figure 3.3: Number of recruits recorded in March and May in seed addition plots located along long-term monitoring transects with various long-term occupancy trends for each of the six native annual forb species. Sample size for each trend category and definitions of these categories described in Table 3.1. “NA” indicates that no transects displayed that occupancy trend for that species.

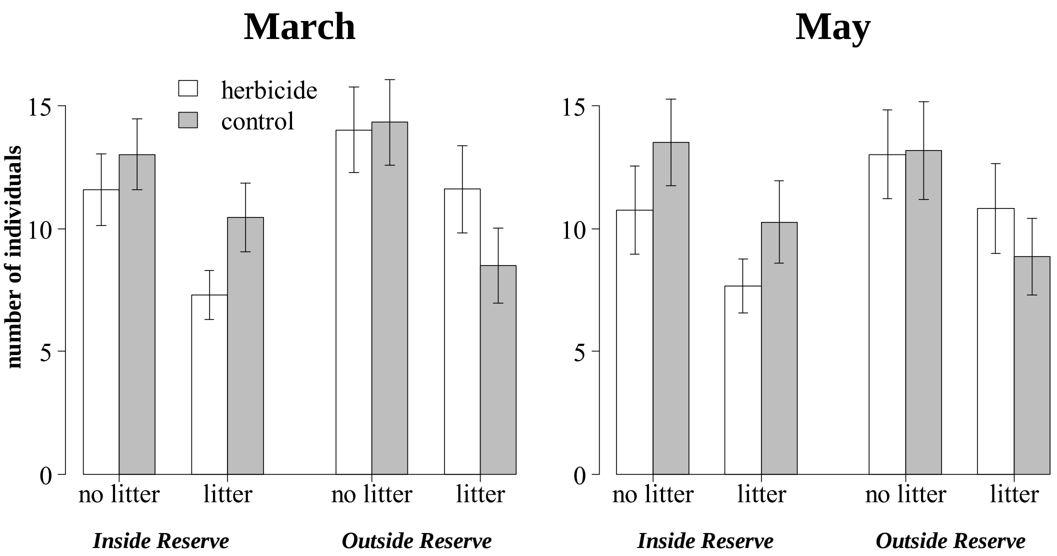


Figure 3.4: Total number of recruits per plot of six native annual forb species recorded in March and May. Seeds for each species were sown into competition removal plots located along long-term monitoring transects inside and outside the reserve boundary. Litter removal and grass-specific herbicide treatments were applied in a factorial design.

4 – Interactive effects of disturbance and nitrogen on species and phylogenetic diversity in California grasslands

Angela J. Brandt, Eric W. Seabloom, and Marc W. Cadotte

ABSTRACT

Disturbance and resource supply can increase or decrease species diversity by altering the relative roles of processes affecting community structure. Examining these effects is important to understand patterns of diversity, as well as how anthropogenic impacts on disturbance regimes and nutrient cycling will affect communities and thus ecosystem functioning. Species diversity may not fully capture community diversity, however, because species are not independent entities but a repository of evolutionary information and relationships, which likely relate to ecological similarity among closely related species. Processes affecting community structure, such as colonization and tolerance of abiotic conditions, likely act on species traits, thus incorporating evolutionary history into studies of biodiversity may increase our power to predict community responses to changing processes, such as disturbance and resource supply. We examined the effects of experimental manipulations of disturbance and nitrogen supply on community diversity and variation among communities in the invaded California grasslands. We used both traditional and phylogenetic diversity metrics of richness, evenness, and community similarity to determine how these processes impacted diversity and elucidate the potential roles of various processes structuring communities. Disturbance increased species richness and evenness. Communities were clustered phylogenetically, however disturbance eroded this clustering. Species composition differed between disturbed and undisturbed communities, and disturbed communities were also more spatially variable in their phylogenetic composition.

Nitrogen supply had little effect on community diversity, but phylogenetic composition was more similar within than among nitrogen treatments. Disturbance and nitrogen interacted in their effects on phylogenetic composition and a combination of disturbance and nitrogen addition decreased species richness. Overall, our results suggest that these grassland communities are structured largely through environmental filtering. Disturbance appeared to increase opportunities for colonization by decreasing competitive effects of resident communities, likely mediated by build-up of exotic grass litter. Further evaluation of the role of dispersal in structuring these communities is necessary, as well as work to relate functional traits to species' phylogenetic relationships.

4.1 INTRODUCTION

Disturbance and resource supply can strongly impact community diversity by influencing mechanisms of community assembly (Hillebrand et al. 2007). Disturbance can promote diversity by maintaining a non-equilibrium state of the community where it reduces abundance of competitive dominants and provides increased opportunities for colonization from the regional species pool (Connell 1978, Petraitis et al. 1989). However, disturbance that increases environmental stress can decrease diversity because taxa that are intolerant of the harsh conditions are excluded (Chase 2007). Likewise, increasing resource supply may increase diversity by providing colonizers with access to resources, or it may decrease diversity by promoting productivity of competitive dominants (Foster and Gross 1998, Hillebrand et al. 2007). Disturbance and resource supply may also interact in their effects on community diversity because disturbances can directly influence resource availability (Reichman and Seabloom 2002) and changes in community structure effected by one process could influence the community's response to other processes (Hillebrand et al. 2007). Understanding the potentially interactive effects of these processes on community diversity has become particularly important given the predominance of anthropogenic influence on disturbance regimes and resource supply, such as through cattle grazing and nitrogen deposition (Weiss 1999, Hayes and Holl 2003a).

Community diversity depends upon recruitment of taxa to communities through dispersal and establishment processes with the potential to filter a subset of species with similar traits from the regional pool or promote differentiation in traits to allow coexistence within the community (Keddy 1992, Weiher and Keddy 1995). The relative roles of different processes structuring communities, such as dispersal, abiotic conditions, and biotic interactions, affect species diversity and variation among communities, and may differ depending upon characteristics of species pools and environmental filters (Chase 2007, Myers and Harms 2009, Chase 2010). For example, if species composition tends to be more similar among communities in certain environmental conditions (i.e., ß-diversity is lower), deterministic processes such as environmental filtering likely play a greater role in assembly because certain traits are necessary for persistence (Chase 2007, 2010). Conversely, if species composition is highly variable among communities, then stochastic processes such as dispersal may be driving assembly (Chase 2007, 2010). However, species diversity may not fully characterize community diversity, and a predictive framework for understanding community assembly and patterns of diversity likely requires a greater focus on species traits (Weiher and Keddy 1995). Species represent a repository of evolutionary information and relationships, and ecological similarity of species is likely related to their evolutionary history (Felsenstein 1985, Prinzing et al. 2001). Assuming that closely related species are similar (i.e., phylogenetic niche conservatism), physiological tolerances may be more similar and interspecific competition stronger among closely related than distantly related species (Webb et al. 2002, Cavender-Bares et al. 2009). Thus, patterns of relatedness might indicate whether community structure depends more upon abiotic conditions or species interactions. For example, communities composed of close relatives may be structured primarily by tolerance to abiotic conditions, while communities composed of distant relatives may be structured primarily by competition (Webb et al. 2002, Cavender-Bares et al. 2009). Phylogenetic community patterns may thus provide further insight into the mechanisms driving community responses to processes of disturbance and resource supply. Furthermore, understanding phylogenetic diversity patterns is itself important because conserving evolutionary information is an important aspect of biodiversity conservation (Faith 1992), and phylogenetic diversity may better predict certain ecosystem processes, such as primary productivity, than species diversity (Cadotte et al. 2008).

Here, we examine the interactive effects of experimentally-manipulated disturbance and resource supply on local community diversity in California grasslands. These grasslands have experienced a dramatic invasion of Eurasian annual grasses and forbs that have dominated the system for over a century (Heady 1977, Hamilton 1997a, Mensing and Byrne 1998). Disturbance and increased nutrient supply generally promote certain functional groups (e.g., exotic annual species) (Foster and Gross 1998, Reichman and Seabloom 2002, Harpole et al. 2007). Thus, exploring the impacts of these processes on diversity in California grasslands is particularly interesting given the predominantly annual nature of the system and the general confounding of perennial life history with native origin in interior grasslands. Exotic annual grasses are associated with a large build-up of plant litter (D'Antonio and Vitousek 1992), which can limit recruitment of many native species (Coleman and Levine 2007, Seabloom 2011). Litter may strongly inhibit native plants relative to exotic plants because the system contains few native annual grasses (Seabloom et al. 2006). Thus, disturbance that reduces litter and increases the amount of bare soil available for colonization, such as cattle grazing, tends to increase species diversity (Hayes and Holl 2003a, Coleman and Levine 2007, Seabloom 2011). However, due to reduced populations of many natives and apparently subsequent seed limitation (Seabloom et al. 2003a, Seabloom et al. 2003b), this increased diversity may not truly represent a greater range of ecological traits or phylogenetic diversity. Nitrogen is an important limiting resource in terrestrial systems (Elser et al. 2007), including California grasslands (Harpole et al. 2007), and high levels of nitrogen deposition occur in many parts of California (Fenn et al. 2003). Increasing availability of nitrogen alters grassland community composition, generally by reducing forb abundance relative to grasses (Foster and Gross 1998, Seabloom et al. 2005, Harpole et al. 2007, Seabloom 2007), and can facilitate invasion of historically resistant communities, with implications for dynamics at higher trophic levels (Weiss 1999, Going et al. 2009).

We applied disturbance (control or removal of all vegetation) and nitrogen (carbon addition, control, or nitrogen addition) treatments in a factorial design to grassland plots located at three California reserves to examine their effects on local diversity and variation in diversity across the region. Our objectives were to determine 1) how disturbance and resource supply affected community diversity and variation among communities, and 2) whether incorporating evolutionary history of taxa, in the form of phylogenetic relatedness, provided additional evidence of the mechanisms driving community assembly under different conditions. We made the following predictions:

Prediction 1: Disturbance will increase species diversity, phylogenetic diversity, and variability among communities.

Rationale.—We predict that species diversity (richness and evenness) will increase immediately following the disturbance due to a reduction in litter-mediated competition and increased space for colonization (Foster and Gross 1998, Coleman and Levine 2007, Seabloom 2011). We expect this effect to attenuate over time as the build-up of litter and increasing light limitation causes communities to converge. We predict phylogenetic diversity in undisturbed plots to be low relative to that expected from a null model of community assembly because biotic conditions, including the build-up of plant litter, may provide a strong filter of the regional species pool and closely related taxa with similar traits may be most successful in these plots (Webb et al. 2002, Dinnage 2009). The roles of other factors, such as colonization and abiotic environmental heterogeneity, may increase in importance in disturbed plots, thus we predict phylogenetic diversity in these communities will more closely resemble a null expectation (Helmus et al. 2007, Dinnage 2009). We predict that species composition will differ between disturbed and undisturbed communities, and that disturbed communities will be more variable in composition, because of the potential for colonization to play an increased role in assembling these communities (Chase 2007, Myers and Harms 2009). We expect that incorporating phylogenetic information into measures of community similarity will enhance our ability to detect differences among disturbed and undisturbed communities due to the generally closer relationships of dominant exotic species and greater ß-diversity in native species within these grasslands (Cadotte et al. 2010a).

Prediction 2: Increasing nitrogen supply will decrease species diversity, increase phylogenetic diversity, decrease phylogenetic evenness, and increase variability among communities.

Rationale.—We predict that species diversity (richness and evenness) will decrease with increasing nitrogen supply due to increases in exotic grass productivity and concomitant decreases in forb and legume abundance (Foster and Gross 1998, Harpole et al. 2007, Seabloom 2011). We expect this effect to be consistent over the course of nitrogen manipulation in the study. We predict that phylogenetic diversity will be lowest relative to null expectations in plots with reduced nitrogen and will increase with nitrogen supply because competition for nitrogen will be reduced, which may promote colonization by more distantly related species (Going et al. 2009, Chase 2010). Phylogenetic-abundance evenness (the relative abundances of different phylogenetic clades) is likely to decrease with increasing nitrogen supply, however, due to high productivity of specific clades (e.g., grasses). We predict that community composition will differ among treatments because species and clades are differentially limited by nitrogen (Seabloom et al. 2003b, Harpole et al. 2007, Going et al. 2009). We expect variability among communities with higher nitrogen supply to increase because of an increased role for colonization in structuring those communities (Chase 2010, but see Myers and Harms 2009).

Prediction 3: In disturbed plots, increasing nitrogen supply will increase species diversity. Communities with the highest nitrogen supply will be the most *variable because species composition will differ between disturbed and undisturbed plots receiving nitrogen augmentation.*

Rationale.—The effect of resource supply on species richness depends in part on the evenness of producer communities (Hillebrand et al. 2007), thus if evenness is higher in disturbed communities, increased nitrogen supply may increase species richness in these communities but not in undisturbed communities. Disturbance and nitrogen addition may interact in their effects on community composition because certain species may only benefit from nitrogen addition when competition is reduced (Foster and Gross 1998, Going et al. 2009). We predict community variability to be highest in disturbed plots with augmented nitrogen because both processes are likely to increase colonization success (Chase 2007, Myers and Harms 2009, Chase 2010).

4.2 METHODS

We used the unseeded control plots from a large-scale seed-addition experiment to quantify diversity in grassland plots subjected to disturbance and nitrogen manipulations (see Seabloom 2011 for a description of the complete experiment). Data were collected for 7 years at three sites within the University of California's Natural Reserve System that span a 500-km latitudinal gradient: Sedgwick Reserve, Santa Barbara County (34º42´N, 120º2´W); Hastings Natural History Reservation, Monterey County (36º22´N, 121º32´W); and McLaughlin Natural Reserve, Napa/Lake/Yolo Counties (38º52´N, 122º25´W), California, USA.

The experiment was established in a completely randomized block design, with three blocks (5×5 grid of 5×5-m plots) located at each of the three reserves, for a total of nine replicates. Within each block, disturbance and nitrogen treatments were applied in a full factorial design for a total of six treatment combinations. The total sample size for this study was thus 54 plots in each year of sampling ($n = 50$ in 2004, due to missing data). Two levels of disturbance (control or removal of aboveground vegetation via raking) were applied to a 1×1-m subplot within the 5×5-m plot in the fall of 2003. Three levels of nitrogen supply (4 g N m^{-2} yr^{-1} as $CaNO_3$, control, or 80 g C m^{-2} yr^{-1}) were applied to the 5×5-m plot from 2003 through 2007. Carbon was added as ground oat straw (50%), corn starch (30%), and sugar (20%) in the first year, and as 60% corn starch and 40% sugar in subsequent years. Nitrogen addition mimicked aerial deposition rates documented for southern California (Fenn et al. 2003), while the purpose of carbon addition was to reduce plant-available nitrogen at the same rate via microbial activity (reviewed in Perry et al. 2010). We estimated percent areal cover of each plant species in a permanent ½×1-m quadrat within the disturbed subplot within each plot in spring (April-June) of 2004-2010 (see Fig. 2.1 for a depiction of the experimental design). We allowed cover to sum to more than 100% in areas with multi-layer canopies. Plants were identified to the most specific level possible. Twelve total plant observations (each with cover of 1%) over the course of the study were unidentifiable and not included in analyses. Aboveground biomass samples were collected in each treatment plot by clipping two 0.1×1-m strips adjacent to the cover subplot in 2004-2007. These samples were sorted to species in 2004-2006. Biomass samples were dried to constant mass at 70ºC and weighed.

We constructed a phylogeny for the 158 species observed in all plots of the larger experiment (Seabloom 2011) as an estimate of the regional species pool for the plots of interest in this study (see *Appendix I* for a complete species list). We downloaded sequences for five genes with varying rates of evolution (*rbcL*, *matK*, *ITS1*, *5.8s*, and *ITS2*) from GenBank to build the phylogeny (Benson et al. 2005). We found at least one of these genes for 113 species. We used genes from a congener, contribal, or confamilial species for 38 species, using species known to occur at our field sites when possible or species observed in the western United States according to the USDA online PLANTS database (http://plants.usda.gov). We added seven species that had been identified only to genus or family as polytomies with their closest relatives. We also included two outgroup species (*Amborella trichopoda* and *Magnolia grandiflora*) and 20 additional species from underrepresented clades, for a total of 180 species in the phylogeny (*Appendix I*). We aligned gene sequences using MUSCLE (Edgar 2004). We used the PhyML algorithm with a BIONJ starting tree to estimate a maximum likelihood phylogeny with approximate likelihood ratio test (aLRT) scores that provide nodal support values (Guindon and Gascuel 2003, Anisimova and Gascuel 2006). The complete phylogeny with nodal support values is available in *Appendix J*.

All analyses were conducted in R 2.11.1 (R Development Core Team 2010). We used the ape library to read in our phylogeny (Paradis et al. 2004), the vegan library for species diversity calculations and multivariate analysis (Oksanen et al. 2010), the nlme library for mixed effects models (Pinheiro et al. 2010), the picante library for phylogenetic diversity and composition calculations (Kembel et al. 2010), the ecoPD library for phylogenetic evenness calculations (Cadotte et al. 2010b), and the labdsv library for nonmetric multi-dimensional scaling (NMDS) (Roberts 2010).

4.2.1 Treatment effects on diversity

We examined effects of disturbance and nitrogen supply on both traditional diversity metrics and metrics incorporating phylogenetic relatedness between taxa. Nitrogen supply was treated as a continuous variable, with -4, 0, and 4 substituted for carbon addition, control, and nitrogen addition plots, respectively. We calculated species richness and evenness (Pielou’s J) for each plot in each year. We used mixed-effects models to determine the effect of disturbance, nitrogen supply, and their interaction on richness and evenness. We incorporated the experimental design into the model as nested random effects (year nested within plot, plot nested within block, and block nested within site), and included year in a three-way interaction with experimental treatments as a fixed effect. Models were estimated using maximum likelihood and model simplification to remove interactions was evaluated with ANOVA to choose the model with the lowest AIC.

We calculated phylogenetic diversity (PD) for each plot in each year as the sum of phylogenetic branch lengths connecting all species in the plot without including the root of the phylogeny (Faith 1992, Cadotte et al. 2008). Richness and PD were strongly correlated ($r = 0.88$, $P < 0.0001$) and thus responded similarly to experimental treatments. To determine the effect of treatments on PD beyond their effect on richness and quantify phylogenetic clustering vs. overdispersion within communities, we examined how PD of plots deviated from expected PD at the same richness under a null model of community assembly in which any species in the phylogeny, excluding the outgroup species, could colonize the plot with equal probability (Bryant et al. 2008, Kembel et al. 2010). We used the ses.pd function in the R picante library to calculate standardized effect sizes of the deviations of observed PD from the mean expected PD calculated from 999 random draws. We also calculated the phylogenetic-abundance evenness (PAE) in each plot, which estimates how evenly plant abundance is distributed among lineages in the phylogeny (Cadotte et al. 2010b). Evenness and PAE were significantly correlated, but evenness explained relatively little variation in PAE ($r = 0.15$, $P = 0.002$). To determine the effect of treatments on PAE beyond their effect on evenness in species abundances, we constructed a null distribution of PAE values for each plot where observed species abundances in the plot were randomized among the taxa 1000 times. Thus, the abundance distribution within plots was retained, while the phylogenetic structure of the plot was altered. We excluded samples with only one species from all diversity analyses, though including these three observations did not affect richness results.

We examined the effects of disturbance and nitrogen supply treatments on other community responses to evaluate the potential mechanisms driving diversity results. We used mixed effects models to determine the effect of disturbance, nitrogen supply, and their interaction on the total cover of three functional groups: grasses, non-leguminous forbs, and leguminous forbs. We also used mixed effects models to determine the effect of nitrogen supply on total aboveground biomass and litter biomass; we could not determine the effect of disturbance on biomass because samples were collected outside the disturbed subplots. We incorporated the experimental design into the model as nested random effects (year nested within plot, plot nested within block, and block nested within site), and included year in an interaction with experimental treatments as a fixed effect. Model simplification was based on AIC.

4.2.2 Treatment effects on community similarity

We examined whether species composition and phylogenetic composition of communities differed with disturbance and nitrogen supply. We calculated similarity in species composition among pairs of plots within each year of sampling using the Sørensen index, which determines the proportion of species that are shared between the two communities. We calculated similarity in phylogenetic composition among pairs of plots within each year using the PhyloSor index, which determines the proportion of branch length in the phylogeny that is shared by the two communities (Bryant et al. 2008). It is important to note that calculation of these indices did not take species abundances into account. The community similarity within vs. among experimental treatments was assessed for both indices with permutational Multivariate Analysis of Variance (perMANOVA) using the adonis function in the R vegan library. The model for each year's distance matrix included an interaction between disturbance and nitrogen supply, and the *P*-value was calculated using 999 permutations of the similarity matrix. Restricting randomizations within site or block (using the strata argument) gave similar results. To determine whether significant perMANOVA results were due to differences in community similarity within a treatment (i.e., variance), we analyzed the multivariate homogeneity of group dispersions for treatments that differed in community composition using the betadisper function in the R vegan library. This analysis cannot incorporate factorial designs, thus a separate model was used for each experimental variable. A permutation distribution of the *F*-ratio was generated using 999 permutations to calculate *P*-values. To visualize results, we performed NMDS ordinations using the bestnmds function in the R labdsv library. We chose the 2- or 3-dimensional ordination with the lowest stress using 50 random starts and 1000 iterations.

4.3 RESULTS

Only a few observed plants were not identified at least to family; a mean of 0.04 species per plot (range of 0-1) were therefore not included in analyses. Species composition in each plot was 95% annual on average (range of 50-100%), and 4% perennial (range of 0-50%). Many species were observed in only one treatment, and the representation of lineages differed by treatment. For example, species from 24 plant families were observed in undisturbed plots and species from 25 plant families were observed in disturbed plots. Representatives of the Fagaceae and Hydrophyllaceae were only observed in undisturbed plots, while Convolvulaceae, Ranunculaceae, and Violaceae were only observed in disturbed plots. Additionally, the mean richness of the Fabaceae in each plot was lower when nitrogen was added (0.68 ± 0.08) than when nitrogen was reduced (1.40 ± 0.12) or unmanipulated (1.13 ± 0.12).

4.3.1 Treatment effects on diversity

Disturbance increased species richness ($P = 0.01$), except in plots where nitrogen was added ($P = 0.0004$ for interaction between disturbance and nitrogen addition; Table 4.1, Fig. 4.1). Richness varied over time ($P < 0.0001$), but treatment effects were consistent. Communities were phylogenetically clustered in general, and 14% of samples were significantly clustered compared to null expectations of phylogenetic diversity (Fig. 4.1). Significant phylogenetic clustering was about twice as likely in undisturbed plots (18% of samples) than in disturbed plots (10% of samples). The frequency of significant clustering did not differ much among nitrogen manipulation treatments (13% in control and 15% in carbon-addition and nitrogen-addition plots).

Species evenness increased somewhat with disturbance (*P* = 0.06) and varied over time (*P* < 0.0001; Fig. 4.2, Table 4.2). Observed PAE was always higher than expected under a null model of PAE where the observed abundances of taxa within each community was randomized, and was highly variable (Fig. 4.2). Deviations of observed PAE from the null expectation were significant (*P* < 0.05) in approximately 70% of samples, except in the disturbed plots with ambient levels of nitrogen, where only 57% of samples deviated significantly from expectation.

Grass cover was lower in plots with augmented nitrogen (*P* = 0.02) and disturbed plots (*P* = 0.05) relative to control plots (see *Appendix K*). Disturbance generally increased forb cover (*P* = 0.06), but this effect attenuated over time (*P* = 0.05 for the interaction between disturbance and year; see *Appendix K*). Legume (Fabaceae) cover increased when nitrogen supply was reduced (*P* = 0.003 for carbon addition vs. control plot cover) and when plots were disturbed (*P* = 0.06), and there was evidence that the treatments were synergistic in their effects because the highest cover of legumes occurred in plots receiving both treatments (*P* = 0.03 for the interaction between carbon addition and disturbance; see *Appendix K*). The strength of the treatment effects and their interaction varied over time, however (*P* = 0.002 for the interaction between carbon addition and year, *P* = 0.05 for the interaction between disturbance and year, and *P* = 0.02 for the three-way interaction between variables).

Litter biomass was greatest in nitrogen addition plots in the spring following initiation of treatments (*P* = 0.05), but this effect reversed over time (*P* = 0.04 for the interaction between nitrogen addition and year; see *Appendix L*). Total aboveground biomass was also initially greatest in nitrogen addition plots, but differences among treatments were not significant (*P* > 0.6; see *Appendix L*).

4.3.2 Treatment effects on community similarity

Species composition differed among disturbance treatments in the spring following the disturbance (perMANOVA *F*-ratio = 2.23, *P* = 0.05 for 2004 samples), but this effect did not persist over time (perMANOVA *F*-ratio = 0.15-0.62, *P* > 0.6 for other years). This difference between treatments was not due to different levels of variation among communities within each treatment (permutation dispersion *F*-ratio = 2.69, *P* = 0.1). A 3-dimensional NMDS ordination provided the lowest stress (14.2; Fig. 4.3).

Disturbance and nitrogen treatments interacted in their effects on phylogenetic community similarity in the spring following the disturbance (perMANOVA *F*-ratio = 1.62, *P* = 0.01 for 2004 samples) and again 6 years later (perMANOVA *F*-ratio = 1.39, *P* = 0.05 for 2010 samples), but no effect was seen in other years (perMANOVA *F*-ratio = 0.98-1.21, *P* > 0.3). In 2004, disturbed communities were significantly more variable in phylogenetic composition than undisturbed communities (permutation dispersion *F*-ratio = 4.5, *P* = 0.03), while communities within each level of nitrogen supply had similar variation in composition (permutation dispersion *F*-ratio = 0.47, *P*

= 0.6). In 2010, variability among communities did not differ within the nitrogen supply treatments (permutation dispersion *F*-ratio = 0.34, *P* = 0.7) or the disturbance treatments (permutation dispersion *F*-ratio = 0.29, *P* = 0.6). A 3-dimensional NMDS ordination for the 2004 samples had a stress of 28.0, and a 3-dimensional ordination for the 2010 samples had a stress of 29.6 (Fig. 4.4). Phylogenetic composition differed by nitrogen supply two springs after treatments were initiated (perMANOVA *F*-ratio = 1.41, *P* = 0.009 for 2005 samples), but no effect was seen in other years (perMANOVA *F*-ratio = 0.62-1.32, *P* > 0.1). This difference between treatments was not due to different levels of variation among phylogenetic composition within each treatment (permutation dispersion *F*-ratio = 0.50, *P* = 0.6). A 3-dimensional NMDS ordination provided the lowest stress (28.8; Fig. 4.5).

4.4 DISCUSSION

Disturbance generally increased species diversity (Fig. 4.1 and 4.2), as predicted (Seabloom 2011). Communities tended to be phylogenetically clustered relative to expectations of phylogenetic diversity under a null model of community assembly where all species observed throughout the experiment could colonize a plot with equal probability (Fig. 4.1). This result is unsurprising given that many species are only found at one of the three reserves (e.g., 72 species were observed at a single site in the plots examined here) and phylobetadiversity is often high both among and within California grassland sites (Cadotte et al. 2010a). Thus, environmental conditions may drive community structure throughout California grasslands (Webb et al. 2002). However, significant levels of phylogenetic clustering were more common in communities that were left undisturbed, thus species inhabiting those communities tended to be more closely related than expected by chance. Biotic conditions in undisturbed plots, such as high biomass of plant litter and lack of bare ground, may act as a filter that only allows species tolerant of these conditions to establish. Recruitment of many grassland species is limited by litter (Foster and Gross 1998, Coleman and Levine 2007, Seabloom 2011), but the strength of this limitation may differ among species and functional groups as their diversity and abundance tend to be differentially affected by the amount of litter present (Foster and Gross 1998, Hayes and Holl 2003a). This idea is supported by the difference in species composition we observed among disturbed and undisturbed plots the spring after we cleared aboveground vegetation, as well as the decrease in grass cover and increase in forb and legume cover we observed in disturbed plots. Furthermore, disturbed plots were more variable in their phylogenetic composition immediately following disturbance, suggesting that stochastic processes, such as colonization, played a greater role in structuring disturbed communities, while deterministic processes, such as tolerance of environmental conditions, may play a greater role in undisturbed communities (Chase 2007). Previous work has shown disturbance to lead to reduced community variability and more phylogenetic clustering (Chase 2007, Dinnage 2009), but differences in the effects of disturbance on colonization opportunities and requirements of favorable traits for persistence may account for different results among studies. In general, disturbance appears to enhance colonization opportunities for plant communities when dispersal limitation is overcome (Myers and Harms 2009). Thus, disturbance that enhances opportunities for colonization appears to enhance both species and phylogenetic diversity.

Nitrogen supply did not affect species diversity or phylogenetic structure in the plots examined here (Fig. 4.1 and 4.2), though species richness decreased with increasing nitrogen supply for other plots within the larger seed addition experiment (Seabloom 2011). Except for a single year, community composition did not differ by nitrogen treatment. Nutrient addition may have little effect on colonization in plant communities (Myers and Harms 2009) and plant communities are generally co-limited by multiple nutrients (Elser et al. 2007). Furthermore, the abundance of leguminous forbs increased with decreasing experimental nitrogen supply, thus nitrogen supply may have differed less than expected among treatments. An initial increase in the biomass of plant litter accompanied nitrogen augmentation, but overall grass cover, total aboveground biomass, and litter biomass did not increase with nitrogen supply. Thus, our manipulations of nitrogen did not appear to overcome general nutrient limitation to reduce resource competition, nor did they lead to increased productivity in dominant species, which likely explains the observed lack of effects.

Disturbance and nitrogen supply interacted in their effects in different ways on different components of community diversity. Contrary to our predictions, species richness decreased with disturbance in plots with augmented nitrogen, though evenness in these plots had increased relative to the control treatment. Perhaps evenness did not increase sufficiently to offset the negative effects of nitrogen addition on richness. The negative effect of disturbance on grass cover appeared to be counteracted somewhat by nitrogen addition, thus early-germinating, fast-growing grasses may have inhibited germination of other species in these plots via competition for other resources (Dyer and Rice 1999, Coleman and Levine 2007). The greatest increases in species richness and evenness occurred in disturbed plots where nitrogen was reduced (i.e. carbon was added), though the interaction was not significant for evenness. Though not observed here, nitrogen addition tends to promote grass productivity more than forb or legume productivity in California grasslands (Harpole et al. 2007), thus species evenness may generally be inversely related to nitrogen supply. Phylogenetic-abundance evenness (PAE) was highly variable in these grassland communities and often lower than 1, meaning that abundance tended to be clustered into short terminal branches in the phylogeny (Cadotte et al. 2010b). Grasses tended to be more abundant than forbs or legumes, thus dominance by this single plant family affects PAE. Observed PAE was generally high in these grassland communities compared to a random distribution of abundances among taxa within plots, thus more evolutionarily unique information is contained within each plant in these plots than expected by chance. However, significant deviance of PAE from the null expectation was less common for disturbed plots at ambient nitrogen levels than all other treatment combinations. Thus, disturbance alone may not increase the amount of unique evolutionary information contributed by each individual in the community (Cadotte et al. 2010b). Disturbance and nitrogen supply interacted in their effects on phylogenetic community composition; many species and certain plant families were observed in only one treatment combination. Future work would benefit from examining how dispersal and species traits affect recruitment into communities with varying levels of disturbance and nutrients to determine whether chance colonization or niche differences are responsible for these rare species' patterns.

Interestingly, the pulse disturbance we applied had an effect on species richness that persisted for 7 years in this predominantly annual system. Long-term monitoring suggests that California grasslands exhibit transient dynamics even centuries after exotic invasion and decades after anthropogenic disturbance (e.g., cattle grazing) has ceased (Brandt and Seabloom in press), thus disturbance can have lasting effects even when communities are dominated by short-lived species. The effect of disturbance on species evenness appeared to attenuate over time, however, suggesting that species less tolerant of conditions in undisturbed plots will eventually be lost.

Our work suggests that community structure in invaded California grasslands is largely governed by physiological tolerance of species to environmental conditions, potentially due to both abiotic and biotic components of the environment. Disturbance can enhance the role of stochastic processes, such as colonization, when it primarily reduces the competitive effects of dominant species that drive recruitment limitation in much of the regional species pool, such as through build-up of plant litter. Increases in species and phylogenetic diversity at both local and regional scales following such disturbance likely have important implications for biodiversity conservation and ecosystem functioning (Faith 1992, Cadotte et al. 2008). Determining how functional traits relate to these species and phylogenetic patterns is a critical next step in evaluating the predictive power of phylogenetic relationships for species responses and to confirm our interpretation of these patterns in terms of the mechanisms structuring communities because phylogenetic clustering only indicates similarity in traits among species in the community if those traits are phylogenetically conserved (Cavender-Bares et al. 2009).

Dominance of exotic species in California grasslands may also drive phylogenetic patterns, and exotic and native diversity are likely governed by different mechanisms. The native species pool is much more diverse than that of exotics in California, exotic species tend to have larger range sizes, and phylogenetic relationships within groups of exotics and between exotic and native species relate to exotic invasiveness (Seabloom et al. 2006, Strauss et al. 2006, Cadotte et al. 2009, Cadotte et al. 2010a). Additionally, explicitly evaluating the relative role of seed limitation compared to establishment limitation is necessary to better understand community assembly. The diversity of species and traits in the species pool can influence how other processes, such as disturbance and resource supply, affect community diversity (Myers and Harms 2009). Invasion in the California grasslands has led to generally reduced populations of native species, and may thus have enhanced seed limitation for many species (Seabloom et al. 2003a, Seabloom et al. 2003b). For example, native perennial grasses were generally absent from the experimental plots analyzed here, but they were able to establish at many sites when added as seed (Seabloom 2011). Thus, invasion has likely altered the relative importance of dispersal, abiotic conditions, and biotic interactions for community structure in California grasslands. Continued exploration of the roles of these community assembly mechanisms on native diversity in invaded ecosystems is critical to inform conservation practices as anthropogenic effects on processes such as disturbance regimes and resource supply continue to increase.

ACKNOWLEDGEMENTS

We thank the UC Natural Reserve System and staff at the Sedgwick, Hastings, and McLaughlin reserves. Thanks also to T. Yoshida, B. A. Martin, E. C. Orling, and research crews at OSU and UC Santa Barbara for field assistance. S. D. Hacker provided valuable comments on the manuscript, B. McCune provided advice on statistical analysis, and the Cadotte lab at the University of Toronto at Scarborough helped discuss ideas and techniques. Work funded by NSF DEB-0235624 (O. J. Reichman, J. Schimel, and E. W. Seabloom) and DEB-0910043 (E. W. Seabloom and A. J. Brandt), Andrew W. Mellon Foundation (O. J. Reichman and E. W. Seabloom), UC Integrated Hardwood Range Management Program (W. D. Koenig, M. V. Ashley,

E. T. Borer, J. M. H. Knops, E. W. Seabloom, and M. R. Stromberg), and OSU Department of Zoology Research Fund.

Table 4.1: Mixed-effects model results from a spatially nested factorial experiment of the effects of disturbance and nitrogen supply on species richness in grassland communities. Two levels of disturbance (raking and control) and three levels of nitrogen (carbon addition, control, and nitrogen addition) were applied. Nitrogen supply was analyzed as a continuous variable because carbon addition was calculated to reduce plant-available nitrogen by 4 g m^{-2} yr^{-1} and nitrogen addition added 4 g m^{-2} yr^{-1}. Reserve, block within reserve, plot within block, and year within plot are included as random effects. *n* = 371 due to four missing observations and three samples with only one species.

Source	Numerator DF	Denominator DF	F	*P*
Intercept	1	316	60.814	<0.0001
Disturbance	1	42	6.715	0.013
Nitrogen	1	42	1.232	0.273
Year	1	316	37.621	<0.0001
Disturbance × Nitrogen	1	42	14.986	0.0004

Table 4.2: Mixed-effects model results from a spatially nested factorial experiment of the effects of disturbance and nitrogen supply on species evenness in grassland communities. Two levels of disturbance (raking and control) and three levels of nitrogen (carbon addition, control, and nitrogen addition) were applied. Nitrogen supply was analyzed as a continuous variable because carbon addition was calculated to reduce plant-available nitrogen by 4 g m^{-2} yr^{-1} and nitrogen addition added 4 g m^{-2} yr^{-1}. Reserve, block within reserve, plot within block, and year within plot are included as random effects. n = 371 due to four missing observations and three samples with only one species.

Source	Numerator DF	Denominator DF	F	*P*
Intercept	1	315	531.335	<0.0001
Disturbance	1	42	3.658	0.063
Nitrogen	1	42	1.435	0.238
Year	1	315	55.560	<0.0001
Disturbance × Nitrogen	1	42	2.611	0.114
Disturbance × Year	1	315	2.011	0.157

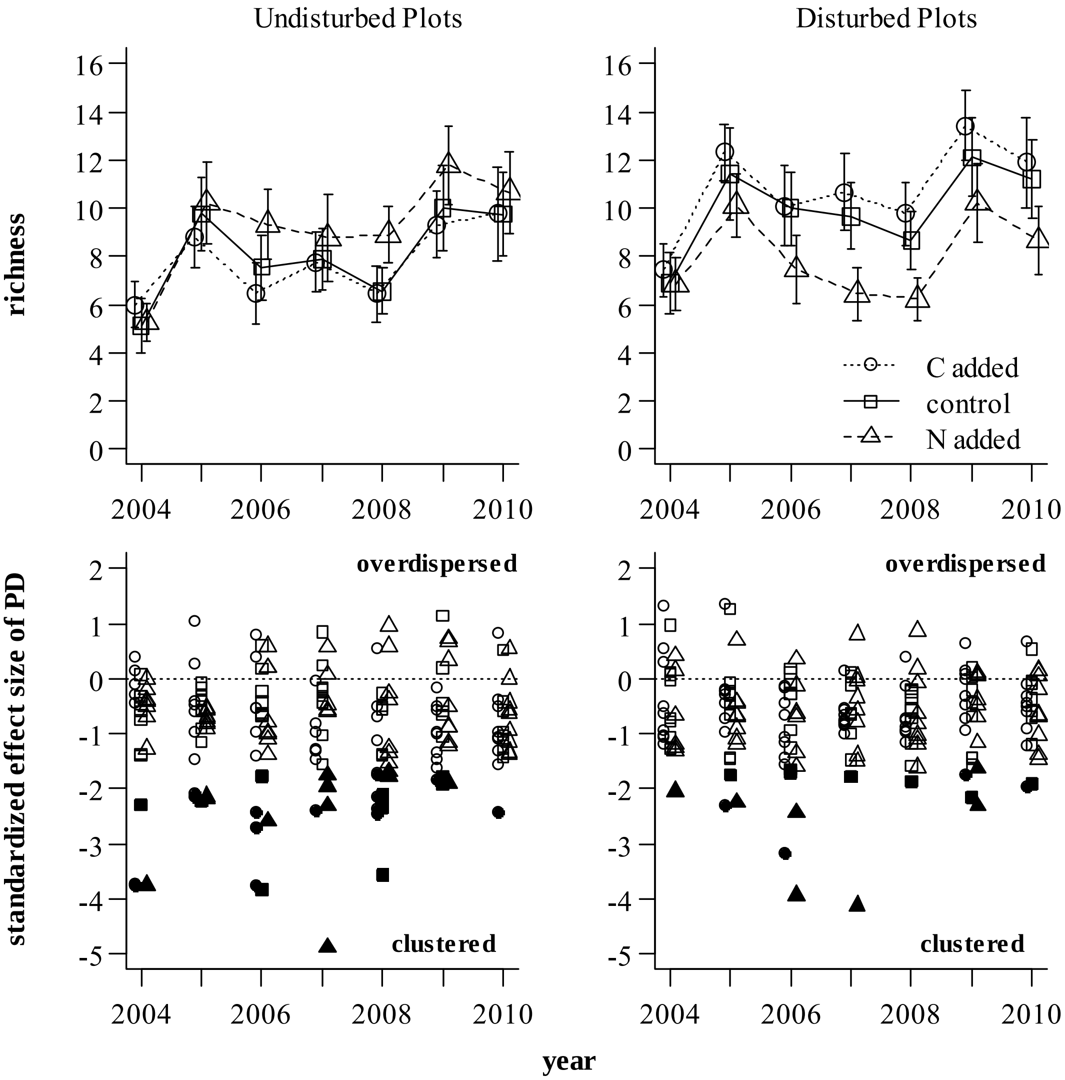


Figure 4.1: Species richness (top row) and the deviation of observed phylogenetic diversity (PD) from the mean of a null model (bottom row) in grassland plots receiving disturbance and nitrogen manipulation treatments in a factorial design and sampled over 7 years. “C addition” represents a nitrogen reduction treatment and “N addition” represents augmentation. Positive standardized effect sizes of PD represent phylogenetic overdispersion in the community and negative effect sizes represent phylogenetic clustering, when compared to null models of random community assembly at the same level of species richness. Significant deviations ($P < 0.05$) from expected PD under a null model of community assembly are represented by solid symbols.

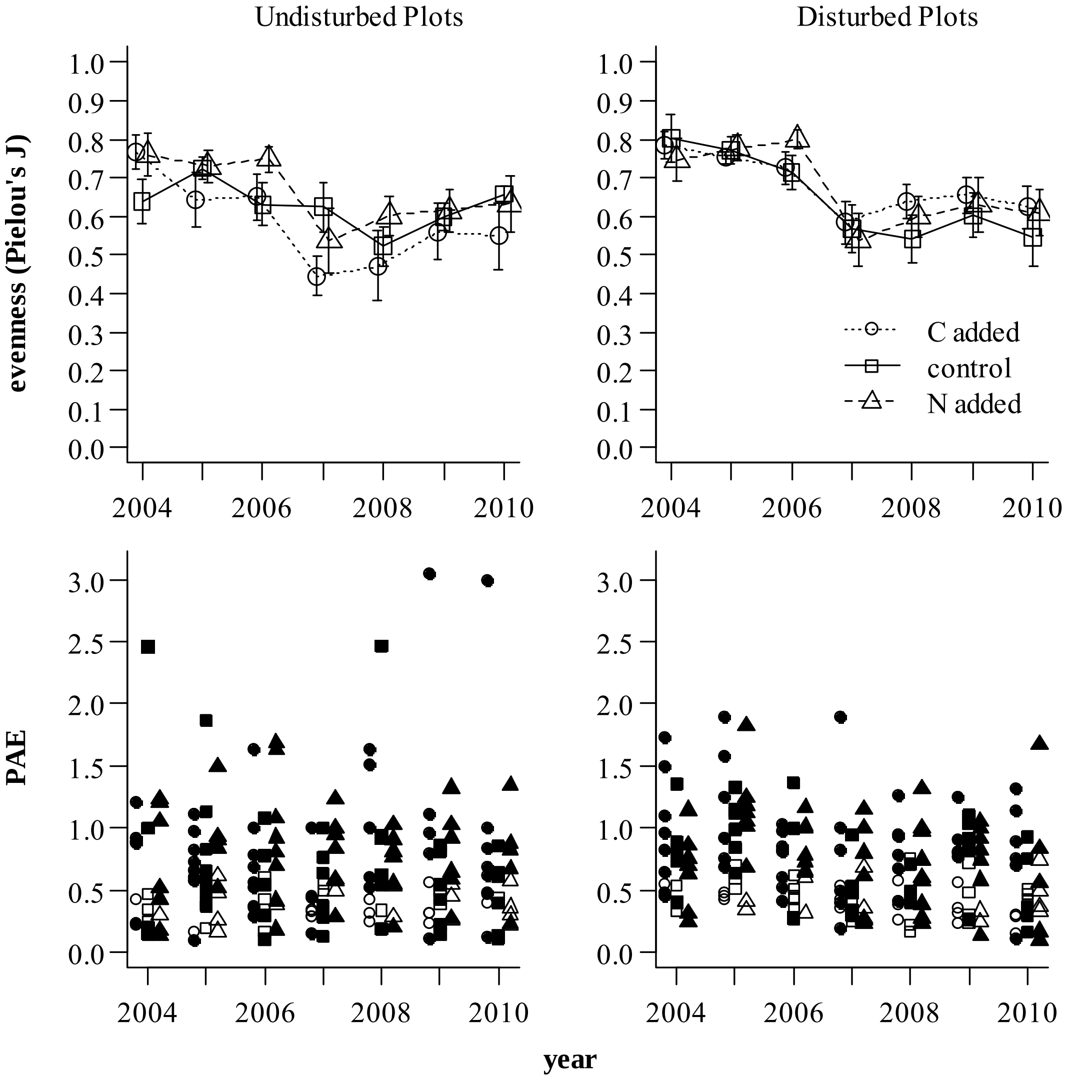


Figure 4.2: Species evenness (top row) and phylogenetic-abundance evenness (PAE) (bottom row) in grassland plots receiving disturbance and nitrogen manipulation treatments in a factorial design and sampled over 7 years. “C addition” represents a nitrogen reduction treatment and “N addition” represents augmentation. Significant deviations (*P* < 0.05) from a null expectation of PAE given a randomized species abundance distribution in the plot are represented by solid symbols.

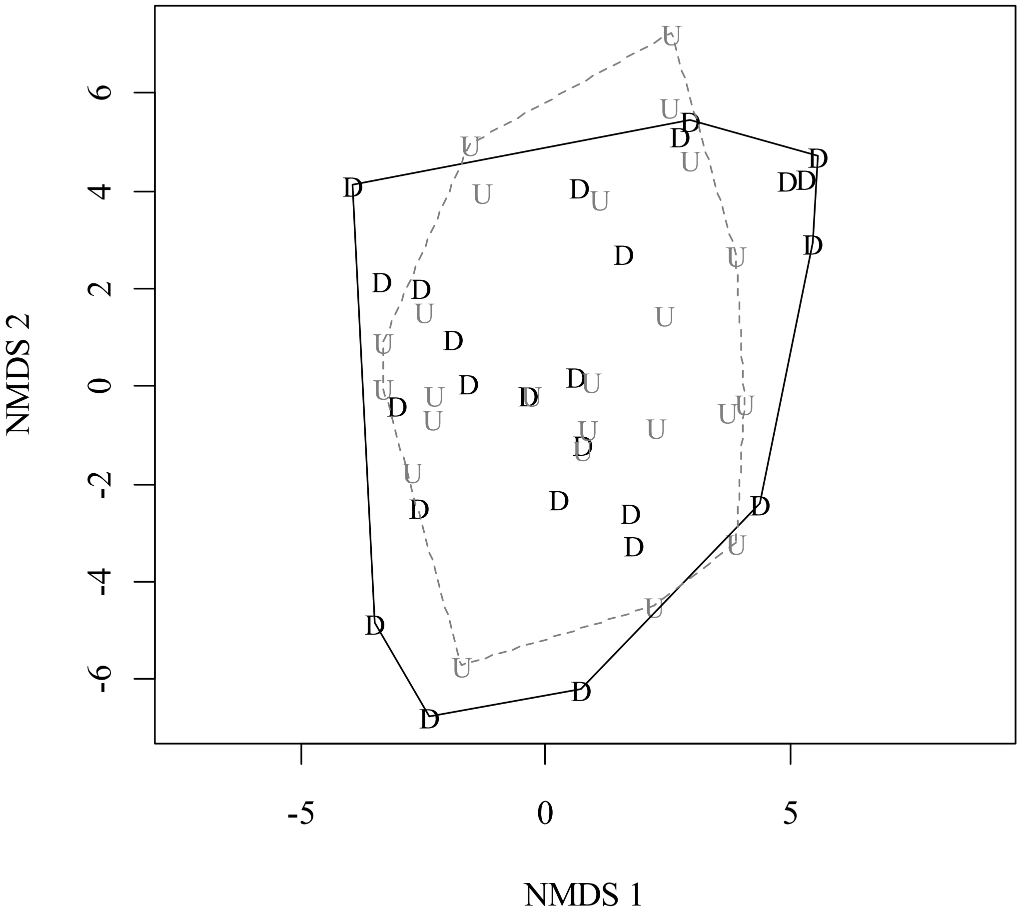


Figure 4.3: Nonmetric multi-dimensional scaling ordination of species composition in disturbed ("D") and undisturbed ("U") grassland plots in 2004 using Sørensen index. NMDS ordination was performed for three axes; here we show the clearest differentiation between groups in the spring following the disturbance treatment.

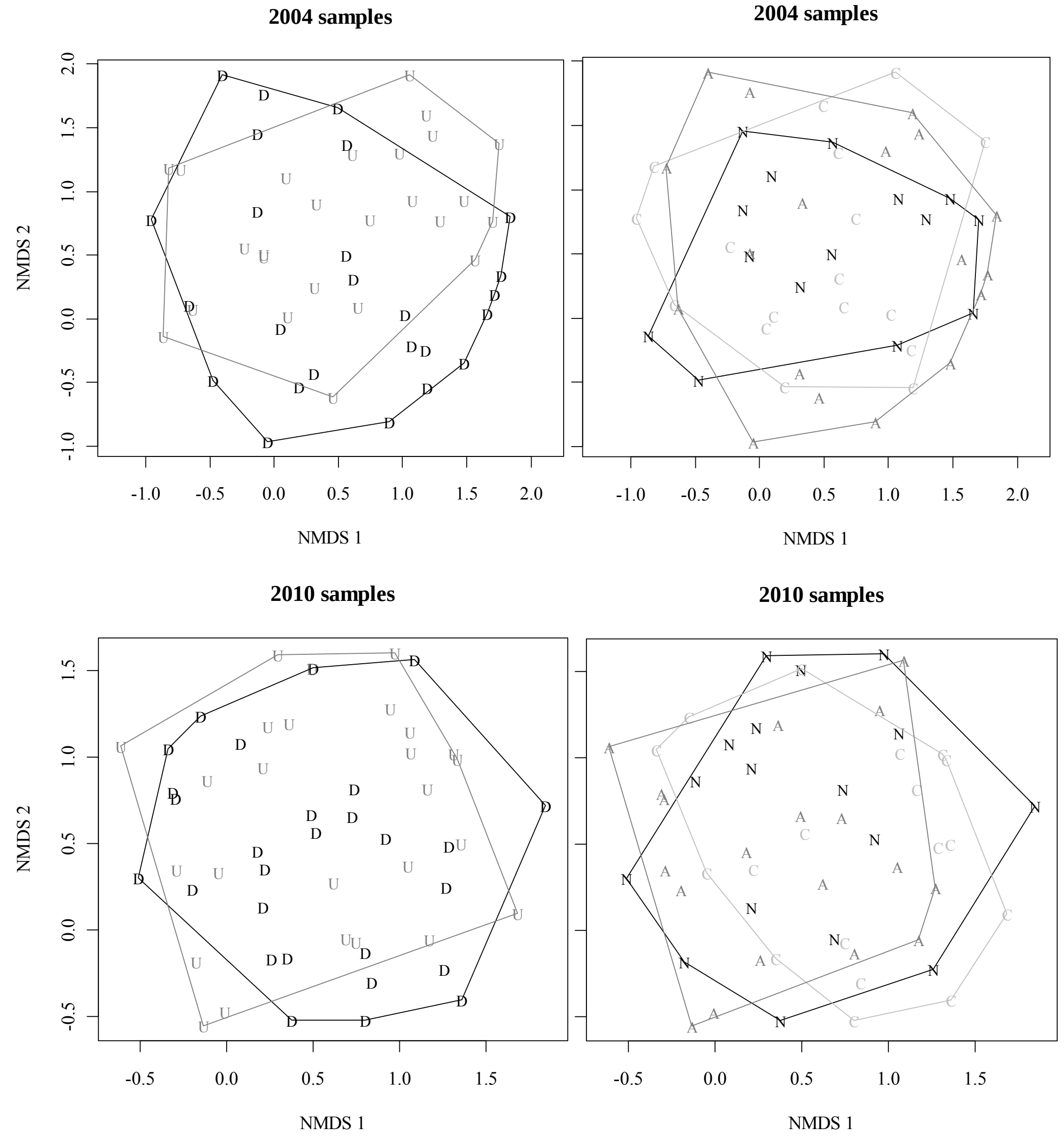


Figure 4.4: Nonmetric multi-dimensional scaling ordination of phylogenetic community composition in grassland plots in 2004 (top row) and 2010 (bottom row) using the phyloSor index. Differences among disturbed (“D”) and undisturbed (“U”) plots are shown in the left column and differences among carbon addition plots (“C”), control plots with ambient conditions (“A”), and nitrogen addition plots (“N”) are shown in the right column. NMDS ordination was performed for three axes in each year; here we show the clearest differentiation between groups.

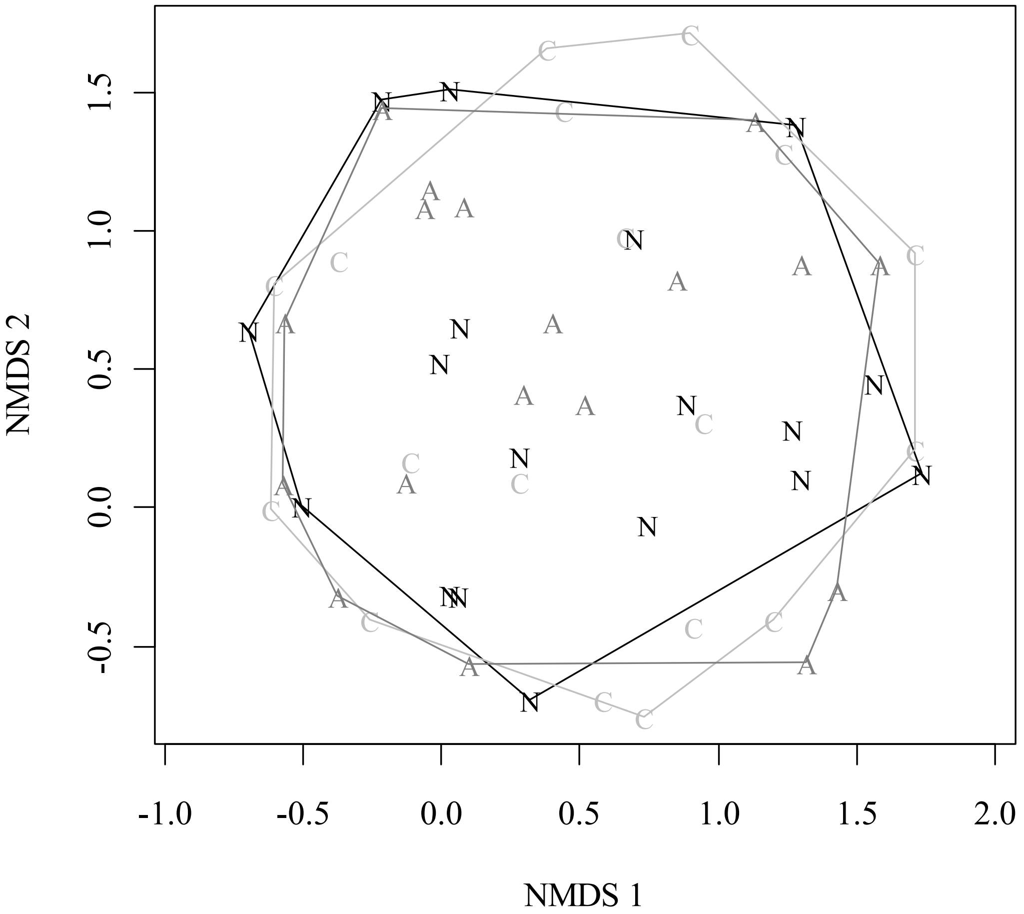


Figure 4.5: Nonmetric multi-dimensional scaling ordination of phylogenetic community composition in grassland plots in 2005 using the phyloSor index to show differences among carbon addition plots (“C”), control plots with ambient conditions (“A”), and nitrogen addition plots (“N”). NMDS ordination was performed for three axes in each year; here we show the clearest differentiation between groups.

5 – Phylogeny and provenance affect plant-soil feedbacks in invaded California grasslands

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Ecology
90(4): 1063-1072
doi:10.1890/08-0054.1

ABSTRACT

Plant–soil feedbacks can affect plant community dynamics by influencing processes of coexistence or invasion, or by maintaining alternate stable states. Darwin's naturalization hypothesis suggests that phylogenetic relatedness should be a critical factor governing such feedbacks in invaded communities but is rarely considered in soil feedback studies. We investigated the effects of soil biota from experimentally established native and invaded California grassland communities on resource capture and allocation of three native and three exotic grass species, comprising three tribes, grown in the laboratory. Phylogeny was the single greatest determinant of grass biomass, root : shoot ratio, and growth rate, with presence of soil biota explaining the second greatest proportion of variance in total grass biomass. Similar trends were observed in soil collected from naturally occurring stands of native perennial and exotic annual grasses. Species of similar life history/provenance exhibited similar biomass responses to the same soil community, while more closely related species exhibited similar root : shoot ratio responses to the same soil community. Relationships between the plant community composition of a field plot and species responses to soil inoculum collected from that field plot were idiosyncratic, with many aspects of plant community structure potentially contributing to soil feedbacks. Thus, future studies should explicitly consider both phylogeny and provenance and evaluate soil feedbacks in a community setting.

5.1 INTRODUCTION

Interactions between above- and belowground biological communities are potential drivers of community and ecosystem dynamics (Wardle et al. 2004). Plants may ‘‘culture’’ the soil biota with which they interact, thus potentially affecting their own growth and demography as well as that of other plant species through feedback loops (Bever et al. 1997, Bever 2003). Negative feedbacks ultimately result in a decline in a plant’s population growth rate, while positive feedbacks ultimately result in an increase in population growth rate (Bever et al. 1997, Bever 2003). Such feedbacks may lead to various community dynamics including coexistence, invasion, or alternate stable states.

Direct negative soil feedbacks, in which a plant’s performance is reduced when grown in soil cultured by conspecifics relative to soil cultured by heterospecifics, are commonly observed and may be important as a mechanism of plant species coexistence (e.g., Bever 1994, Holah and Alexander 1999, Klironomos 2002, De Deyn et al. 2003, Callaway et al. 2004b). The potential for negative feedbacks to promote coexistence has been demonstrated using models (Bever et al. 1997, Bever 2003, Bonanomi et al. 2005), field observations (Klironomos 2002), and mesocosm experiments (De Deyn et al. 2003). Positive soil feedbacks are also common (Klironomos 2002, Callaway et al. 2003, Callaway et al. 2004a, Reinhart and Callaway 2004), but are only likely to lead to plant species coexistence at larger spatial scales (Bever et al. 1997, Bever 2003).

Soil biota may facilitate biological invasions when species of different provenance (i.e., native and exotic) have distinct responses to soil biota. A reduction in pathogen or consumer pressure, acquisition of mutualistic interactions, or a combination of these factors in the introduced range of a species may lead to positive soil feedbacks, thus promoting invasion success (see Mitchell et al. 2006 for a review of invasion mechanism hypotheses). Soil feedbacks for exotic plants can be more positive in their introduced vs. their native ranges (Callaway et al. 2004b, Reinhart and Callaway 2004) and compared to native species in their introduced ranges (Klironomos 2002, Agrawal et al. 2005, Van der Putten et al. 2007). Both release from soil pathogens (Van der Putten et al. 2007) and benefits from soil mutualists within an introduced range (Callaway et al. 2003, Callaway et al. 2004a) appear capable of leading to positive soil feedbacks for exotic plants, with the potential to act synergistically (Klironomos 2002, Callaway et al. 2004b, Reinhart and Callaway 2004). Furthermore, exotic plants may alter composition of the soil biota with the potential to enhance population growth of conspecifics or other exotics (Klironomos 2002, Callaway et al. 2004b, Hawkes et al. 2005, Van der Putten et al. 2007). Empirically documented positive soil feedbacks for exotic plants are likely too weak to promote invasive spread, but may increase invader impact through increases in plant density (Levine et al. 2006).

Though previously unexplored, soil feedbacks could contribute to alternate stable states of a community. Alternate stable states can arise when two species are effectively prevented from invading established populations of the other (MacArthur and Levins 1967, Gurney and Nisbet 1998). Such invasion may be prevented via feedbacks between biotic and abiotic factors in the environment (Suding et al. 2004), or if positive intraspecific interactions strengthen priority effects (Molofsky and Bever 2002). Positive soil feedbacks, particularly coupled with local dispersal, could contribute to a mosaic of monospecific stands resistant to invasion (Bever et al. 1997) and, therefore, to alternate stable states of the community. Concurrent or subsequent negative feedbacks to heterospecifics could further inhibit invasion of established populations. The potential for soil feedbacks to maintain alternate stable states seems plausible as plant species abundances in the field correlate positively with soil feedbacks, while negative soil feedbacks appear to maintain plant rarity (Klironomos 2002); but this remains to be tested.

Understanding effects of soil feedbacks in invaded communities could provide important insight into invasion and restoration ecology, because of their potential to affect processes of coexistence, invasion, and alternate stable states. However, soil feedbacks can be affected by both the provenance and phylogenetic relatedness of plants; thus both of these factors must be considered in any study of soil feedbacks. Phylogeny cannot be ignored because species responses are not statistically independent (Felsenstein 1985) and phylogeny may affect gains and losses of biotic interactions when an exotic species is introduced to a novel environment (Mitchell et al. 2006). However, the impact on invasion success of an invader’s phylogenetic relatedness to community residents is under debate (Richardson et al. 2000, Daehler 2001). Darwin's naturalization hypothesis posits that invaders closely related to residents are less likely to successfully invade because they are more likely to gain negative interactions in their introduced range (Daehler 2001, Agrawal et al. 2005, Mitchell et al. 2006). Some support for this view has been found in plants, where ''invasiveness'' is negatively correlated with the phylogenetic relatedness of exotic species to natives (Strauss et al. 2006). Alternatively, plant invaders closely related to residents may have a greater chance of gaining positive interactions in their introduced range, and thus may be more likely to successfully invade (Richardson et al. 2000). Thus, phylogeny seems an essential consideration in studies comparing interactions of native and exotic plants with soil biota.

We propose three criteria necessary for soil feedbacks to play a significant role in plant community dynamics: (1) the soil biota must have a strong effect on plant performance relative to other factors, thus being capable of altering the plant's population growth rate to affect community processes as presented in previous modeling work (Bever et al. 1997, Bever 2003); (2) plant species must exhibit differential responses to a soil community (Bever 2003); and (3) the effects of soil biota from entire plant communities of varying composition must differ predictably for different species groups (e.g., natives vs. exotics), because both plant diversity and identity can influence soil feedbacks (Bartelt-Ryser et al. 2005). These criteria are hierarchical in importance, because if the first is not met, the others become moot.

Though many studies have investigated one or more of these criteria, rarely have all three been tested simultaneously (Olff et al. 2000). Only one previous study, to our knowledge, has examined the effect of plant community composition in the field, but with highly manipulated communities (Bartelt-Ryser et al. 2005). The soil feedbacks literature would thus greatly benefit from further investigation of plant community effects on soil feedbacks. Furthermore, soil feedback studies have rarely considered effects of phylogeny and provenance together (Agrawal et al. 2005).

Here, we examine the potential for soil feedbacks to drive community dynamics in California grasslands, a system in which over 9.2×10^6 ha have been converted from domination by native perennials to domination by exotic annuals (Heady 1977). This system provides a useful model for exploring soil feedbacks in an invaded ecosystem because many of California's exotic grasses are closely related to natives (Strauss et al. 2006), but differ in life history. Provenance may thus play a greater role in soil feedbacks in California grasslands than in other systems with closely related native and exotic species. Furthermore, common exotic grasses in California can alter soil communities of ammonia-oxidizing bacteria (Hawkes et al. 2005) and communities of arbuscular mycorrhizal fungi infecting native plant roots (Hawkes et al. 2006), suggesting that native and exotic species differ in their interactions with soil biota.

We compare the effects of soil feedbacks on three critical aspects of species performance, resource capture (i.e., total plant biomass), resource allocation (i.e., root

: shoot ratio), and rate of resource capture (i.e., time to half of maximum height and maximum growth rate), for three native perennial and three exotic annual California grasses comprising three tribes. We explicitly test the three preconditions for significant effects of soil feedbacks on community dynamics established above by determining: (1) the effect of soil biota on plant performance relative to phylogeny and life history/provenance; (2) whether species exhibit differential responses to the same soil collection and if those responses vary by phylogeny or life history/provenance; and (3) how plant community composition and change affect the soil feedback, particularly when the community is composed of species with similar phylogeny or life history/provenance. Our approach is unique as it draws together in one case study many aspects of examining plant–soil feedbacks within the context of whole communities and Darwin's naturalization hypothesis. We used experimentally established plant communities to achieve a balance between realistic levels of complexity and control. We also compared trends from our experimental communities to responses in soil from communities that differ naturally in exotic annual grass dominance.

5.2 METHODS

Grasses were grown individually in pots in the laboratory in soil collected from experimental plots at the University of California Sedgwick Reserve, Santa Ynez, California, USA (34º42'30" N, 120º2'30" W). In January of 1998, we plowed a recently abandoned agricultural field at the reserve and seeded it with five native perennial grasses. The site is located on a floodplain terrace and soil is a low-nutrient sandy clay loam (Seabloom et al. 2003b). In 2000, we established three plant community treatments as part of a larger invasion experiment: (1) a native perennial grass-dominated community, which received no further seeding; (2) exotic annual grass-dominated community, which was treated with herbicide in 1999 and seeded with exotic annual grasses; and (3) exotic annual grass communities seeded with native perennial grasses, which were treated as in (2) and seeded with native perennial grasses in fall 2000 (see Seabloom et al. 2003b for a complete description of this experiment). Seeding native perennial grass-dominated plots with exotic annual grasses had no effect on perennial or annual grass biomass (Seabloom et al. 2003b); thus we did not include this treatment in the current study. Seed addition treatments effectively eliminated recruitment limitation in these plots; thus biotic interactions were the primary determinant of community structure. In spring of 2001–2005, two 1.0 × 0.1 m strips of vegetation in each experimental plot were clipped at the soil surface, sorted to species, dried to constant mass, and weighed to estimate the plot's plant community composition (see *Appendix M* for biomass of six focal species in the three plant community treatments over time).

Laboratory experimental methods generally follow those of Bever (1994). On 29 November 2005 we collected 1 L of soil from the top 10 cm of 24 field plots (i.e., eight plots from each plant community treatment) and additional soil adjacent to the experimental plots to use as sterile background soil. Soil was also collected from eight plots within naturally occurring grass stands, four each from an exotic annual stand and a native perennial stand, to determine whether observed trends were an artifact of using soil from experimental communities. Field soil was shipped overnight to Oregon State University, Corvallis, Oregon, and potted within three days. Background soil was autoclaved for sterilization. All field soil (unsieved and including small roots) was mixed in a 1:1 ratio with autoclaved river sand before potting. Soil mixtures were potted in D40 Deepots (656 mL; Stuewe and Sons, Tangent, Oregon, USA) with mesh and 50 mL of sand lining the bottom. Support trays held pots 2 cm above water trays to prevent cross contamination. Background soil (200 mL) was placed in the top and bottom thirds of each pot to minimize abiotic differences between soil treatments. Soil from each field plot (200 mL) was placed in the middle third of each treatment pot as whole-soil inoculum. Controls contained 600 mL of sterile background soil. Pots were arranged randomly on laboratory benches under fluorescent growth lights set to a 12:12 photoperiod, with supplemental light from west-facing windows.

We grew three exotic annual grasses (*Bromus hordeaceus*, *B. madritensis*, and *Hordeum murinum*) and three native perennial grasses (*B. carinatus*, *Elymus glaucus*, and *Nassella pulchra*) separately in each soil sample from the field plots and eight control pots per species, for a total of 240 pots. All seed was collected by hand in California. These species represent three phylogenetic tribes within the Poaceae: Bromeae (*Bromus* spp.), Triticeae (*E. glaucus* and *H. murinum*), and Stipeae (*N.*

pulchra) (Peterson and Soreng 2007). No other species of Stipeae were present in the experimental plots from which soil was collected. Grass species were chosen to represent a suite of commonly observed species in the experimental and natural communities at Sedgwick and elsewhere in California. For example, these six species comprised 75% ± 2% of the total biomass at the field site from 2001–2005 (E. W. Seabloom, *unpublished data*). Though the provenance and life history of the grasses are confounded, this is representative of the inland California grasslands system, which contains very few native annual or exotic perennial grasses, none of which were detected in the plots from which we collected soil. Seeds were germinated on paper towels in the laboratory and planted in randomly selected pots by 19 December 2005. Grasses were watered as needed and, after approximately five weeks, fertilized every two weeks with 25 mL of a 1.3% solution of 1.4:0.2:0.2 liquid fertilizer (Coast of Maine Fermented Salmon Organic Fertilizer; Coast of Maine Organic Products, Portland, Maine, USA).

Maximum height of each grass (i.e., maximum blade length or height of reproductive stem, if applicable) was recorded twice weekly for the first five weeks and weekly for the remainder of the experiment. After ~3.5 months (prior to senescence), aboveground biomass was clipped at soil level and roots were washed. We examined this life stage because survival from the first to second growing season represents a critical bottleneck for California's perennial grasses (e.g., Hamilton 1997b, Brown and Rice 2000) and can be strongly affected by seedling establishment rates (Shoulders 1994). Modeling work with these perennial grasses has shown that survival to subsequent years critically impacts long-term fitness (Borer et al. 2007). Shoot and root biomass were dried to constant mass at 70ºC and weighed. Total biomass and root : shoot ratios for each grass plant were calculated as estimates of resource capture and allocation, respectively. We fit von Bertalanffy growth curves to the time series data of maximum height for each grass plant (Gurney and Nisbet 1998). We fit both a four parameter model (initial height, final maximum height, time to half of final maximum height, and maximum growth rate) and a three parameter model (the same, except initial height assumed to be zero). When both models successfully fit the data, we chose the model with the lowest AIC (Akaike's Information Criterion) score. We used the time to half of maximum height and maximum growth rate parameters as estimates of the rate of resource capture for each grass plant. Initial height was ignored in statistical analyses as a nuisance parameter and total biomass measurements were analyzed in place of the final maximum height parameter. All statistical analyses were performed in R (R Development Core Team 2010). Four grass individuals were excluded from analyses of soil from experimental community plots due to mortality (see *Appendix N* for sample sizes). One individual was excluded from analyses of soil from natural community plots due to mortality and another from analyses on growth rate variables because its parameters could not be determined (see *Appendix O* for sample sizes).

5.2.1 Relative effect of soil biota on plant performance

We used analysis of variance (ANOVA) to test for effects of tribe, species nested within tribe, life history/provenance, presence of whole-soil inoculum, and interactions between presence of inoculum and the other three explanatory variables on total biomass, root : shoot ratio, time to half of maximum height, and maximum growth rate. Orthogonal contrasts were performed to determine significant differences between each of the three tribes. Though grouping by tribe is a limited measure of phylogenetic relatedness, grouping is valid when comparing effects of phylogeny with effects of other factors and one can assume that species within groups are more closely related than species of different groups (Silvertown et al. 2006). Presence of whole-soil inoculum was used as a factor rather than field plot community treatments because of high variability in species biomass among plots (see *Appendix M*). Diagnostic plots were examined to ensure that assumptions of ANOVA were met. The proportion of the variance explained by each predictor was calculated. We also performed ANOVA on responses of grasses grown in soil collected from the natural communities to compare trends observed in the soil of experimental communities.

5.2.2 Differential responses of species to soil collections

The four response variables (total biomass, root : shoot ratio, time to half of maximum height, and maximum growth rate) were standardized to compare species responses to each soil sample and determine whether responses to soils from the same plot were more similar for species within phylogenetic or life history/provenance groups. Response variables were standardized to reflect the relative difference from the control treatment ([treatment value – mean of control]/grand mean for species), a method of adjusting experimental treatment effects for systematic variation among species to allow direct comparisons (Cochran and Cox 1992). Correlation matrices for each standardized response variable were constructed to provide pairwise comparisons of the response of each species to each inoculums sample. Significant difference from zero was tested for each Pearson product-moment correlation. Mantel tests (with 1000 permutations) were used to compare each of these correlation matrices to phylogenetic and life history/provenance group matrices, thus determining if the correlation between the responses of two species to the same soil sample was more positive if the two species were more closely related or of like life history/provenance, respectively. Others have similarly used Mantel tests to compare phylogenetic relatedness and similarity in species traits (Böhning-Gaese et al. 2006). Two phylogenetic matrices were constructed, one comparing species within vs. between tribes and one using phylogenetic distances. In the tribe-comparison matrix, cells comparing species in the same tribe had a value of one and all other cells had a value of zero. For the second phylogenetic matrix, we constructed a phylogenetic distance matrix using publicly available sequences of NADH dehydrogenase subunit F in MEGA 4.0 (Tamura et al. 2007). We substituted sequences from *Bromus rubens* for *B. madritensis*, four *Elymus* species native to the western United States for *E. glaucus*, and *Nassella viridula* for *N. pulchra* because no information was available for these three species. We used negative distances in this matrix to test the hypothesis that more closely related species would have more similar responses to the same soil inoculum. In the life history/provenance group matrix, cells comparing species of the same life history/provenance had a value of one and all other cells had a value of zero.

5.2.3 Plant community effects on soil feedbacks

The effects of current plant community composition and change over time in study species abundances in plots from which soil was collected were examined for the four standardized response variables, thus specifically testing the effect of inoculum from these communities on plant performance. First, the effects of current plant community composition were tested using multiple regression on the spring 2005 biomass of conspecifics, contribal species, exotic annual grasses, and native perennial grasses, presence/absence of each study species, and species richness in the plot from which soil was collected. Presence/absence of *B. hordeaceus* was not included in the analysis because it was present in all field plots. Diagnostic plots were examined to ensure that the assumptions of multiple regression were met. Variables with high variance inflation factors (defined as VIF > 10) were removed from the model to prevent multicollinearity. Second, we tested whether species performance in the field could predict individual grass performance in the laboratory. We compared the change over time of the species abundance of a grass in a field plot to the standardized responses of an individual of the same species grown in soil collected from that plot using Pearson product-moment correlations. Long-term (2001–2005) and recent (2004–2005) changes in species biomass in field plots were standardized by dividing the slope of a linear regression of species biomass in the plot over time (for five or two years, respectively) by the mean biomass of the species in the plot over the five-year period.

5.3 RESULTS

5.3.1 Relative effect of soil biota on plant performance

Tribe explained the greatest proportion of variability in total grass biomass, root : shoot ratio, and maximum growth rate (Fig. 5.1), though most of the difference in biomass and root : shoot ratio was due to *N. pulchra* ($P < 0.00001$ from orthogonal contrasts). Presence of whole-soil inoculum and the interaction between inoculums and species within a tribe explained the second greatest proportion of variability in total grass biomass (Fig. 5.1). Overall, the effect of whole-soil inoculum on individual grass biomass ranged from negative to neutral ($P < 0.00001$ for inoculum main effect; $P = 0.00001$ for inoculum × species interaction). Effect of inoculum was strongest for *B. carinatus* and *H. murinum*, whose mean biomass was reduced by 38% and 47%, respectively, when grown in non-sterile vs. sterile soil (see *Appendix N* for a summary of responses by species).

Life history/provenance explained the second greatest proportion of variability in root : shoot ratio, followed by species nested within tribes (Fig. 5.1). The mean root : shoot ratio of perennial grasses was 11% greater than that of annuals, a significantly greater allocation to root biomass ($P < 0.0001$). Overall, the presence of whole-soil inoculum did not significantly affect resource allocation of grasses ($P = 0.09$) as its effects ranged from negative to positive for different species ($P = 0.02$ for inoculum × species interaction). Mean root : shoot ratios of *B. carinatus*, *B. madritensis*, and *H. murinum* were reduced by 19–31% when grown in non-sterile vs. sterile soil, while the mean root : shoot ratio of *B. hordeaceus* increased by 11%, and *E. glaucus* and *N. pulchra* were not affected (see *Appendix N*).

Time to half of maximum height was not well-explained by factors included in this analysis (Fig. 5.1). Life history/provenance explained the second greatest proportion of variability in maximum growth rate, followed by species within tribes (Fig. 5.1). The maximum growth rate of exotic annual grasses was 40% greater than native perennial grasses ($P < 0.00001$). Effects of whole-soil inoculum on time to half of maximum height and maximum growth rate ranged from negative to positive for different species ($P = 0.009$ and 0.03, respectively, for tribe × inoculum interactions). Mean time to half of maximum height decreased by 16% for *B. madritensis* and 90% for *N. pulchra* in non-sterile vs. sterile soil, while it increased for *E. glaucus* by 33% and *H. murinum* by 44%. Mean maximum growth rate of *N. pulchra* decreased by 42%, while growth rate of *B. hordeaceus* increased by 17% in non-sterile vs. sterile soil (see *Appendix N*).

Trends similar to those described above were observed for grasses grown in pots containing whole-soil inoculums from natural communities (see *Appendix O* for a summary of responses by species). In particular, tribe explained the greatest proportion of variability in biomass and root : shoot ratio ($P < 0.00001$), and the second greatest proportion of variability in maximum growth rate ($P < 0.001$). Presence of inoculum explained the second greatest proportion of variability in biomass, with a significant decrease in biomass observed when inoculum was present ($P < 0.00001$), but the interaction between presence of inoculum and species nested within tribe was significant ($P < 0.01$). Life history/provenance explained the greatest proportion of variability in maximum growth rate and second greatest proportion of variability in root : shoot ratio ($P < 0.00001$). Presence of inoculum was also significant for both of these responses ($P < 0.05$). We thus conclude that our findings are not solely an artifact of using soil from experimentally established plant communities in an old field.

5.3.2 Differential responses of species to soil collections

Biomass and root : shoot ratio responses of all species were similar when grown in pots containing whole-soil inoculum from the same field plot (Table 5.1). Species of like life history/provenance exhibited more similar biomass responses ($z = 8.22$, $P < 0.0001$), while species within tribes did not ($z = 7.19$, $P = 0.20$; see Table 5.1). However, biomass responses appeared somewhat more similar for species separated by shorter phylogenetic distances ($z = -0.085$, $P = 0.06$). Species within tribes ($z = 7.92$, $P = 0.03$) and species separated by shorter phylogenetic distance ($z = -0.24$, $P = 0.002$) exhibited more similar root : shoot ratio responses, while species of like life history/provenance did not ($z = 8.15$, $P = 0.49$; see Table 5.1). Time to half of maximum height and maximum growth rate of each species were not correlated with responses of other species grown in the same soil collection ($P > 0.06$). Time to half of maximum height and maximum growth rate were not more similar among species within either phylogenetic ($z = 6.20$–6.30, $P > 0.5$ for tribe comparisons and $z = -0.047$ to -0.053, $P > 0.1$ for phylogenetic distance comparisons) or life history/provenance groups ($z = 5.76$–6.64, $P > 0.4$).

5.3.3 Plant community effects on soil feedbacks

Relationships between the plant community composition of a field plot and species responses to soil inoculum collected from that field plot were idiosyncratic. However, the change in species abundances over time in field plots did not correlate to species performance in the laboratory when grown in soil collected from those plots ($P > 0.05$).

There were no significant relationships between field community composition and biomass responses of species ($P > 0.05$). Plant community composition had no effect on root : shoot ratio of *E. glaucus*, *H. murinum*, and *N. pulchra* ($P > 0.07$). Root : shoot ratio of *B. carinatus* decreased with increasing biomass of conspecifics ($P = 0.046$) and when *B. madritensis* was present in the field community ($P = 0.003$), but increased when *H. murinum* was present ($P = 0.001$). Root : shoot ratio of *B. hordeaceus* decreased with increasing biomass of contribal species in the field community ($P = 0.03$). Root : shoot ratio of *B. madritensis* increased with increasing biomass of native perennial grasses ($P = 0.01$) and decreased when *E. glaucus* was present ($P = 0.03$) in the field community.

Plant community composition had no effect on time to half of maximum height of *B. madritensis*, *E. glaucus*, *H. murinum*, and *N. pulchra* (P > 0.05). Time to half of maximum height of *B. carinatus* increased when *E. glaucus* was present in the field community ($P = 0.03$). Time to half of maximum height of *B. hordeaceus* increased when *N. pulchra* was present in the field community ($P = 0.02$). Plant community composition had no effect onmaximum growth rate of *B. hordeaceus*, *B. madritensis*, and *E. glaucus* ($P > 0.05$). Maximum growth rate of *B. carinatus* increased with increasing biomass of exotic annual grasses ($P = 0.007$) and when *E. glaucus* ($P = 0.0007$), *H. murinum* ($P = 0.014$), and *N. pulchra* ($P = 0.024$) were present in the field community, but decreased with increasing species richness ($P = 0.0006$). Maximum growth rate of *H. murinum* increased when *E. glaucus* was present in the field community ($P = 0.04$), but decreased with increasing species richness ($P = 0.015$). Maximum growth rate of *N. pulchra* increased when *H. murinum* was present in the field community ($P = 0.02$).

5.4 DISCUSSION

We found that field-collected soil inocula samples do indicate that plant–soil feedbacks in an invaded ecosystem affect four aspects of plant performance, and that such effects can vary by plant phylogeny and life history/provenance. We examined three conditions necessary for soil biota to play a significant role in plant community dynamics: (1) the relative effect of soil biota on plant performance, (2) differential responses of species to soil inoculum samples, and (3) the effect of a soil's plant community on soil feedbacks.

5.4.1 Relative effect of soil biota on plant performance

The presence of soil biota was a strong factor in determining resource capture, resource allocation, and growth rates for certain species. Grass biomass generally decreased when soil biota were present, as has been observed for many plant species (e.g., Bever 1994, Holah and Alexander 1999, Olff et al. 2000, Beckstead and Parker 2003, Callaway et al. 2004b, Reinhart and Callaway 2004), and indicates that soil biota have the potential to reduce resource capture in these species. Effects of soil biota on plant resource allocation (i.e., root : shoot ratio) tend to be more species specific (Bever 1994, Holah and Alexander 1999, Olff et al. 2000, Beckstead and Parker 2003), as we also observed. We found that different aspects of plant growth rates can be affected by the presence of soil biota, but effects differ by species. Holah and Alexander (1999) also observed growth effects of soil biota to vary by species, but did not explicitly examine growth rates. The variability we observed in species responses to soil biota suggests that effects of soil biota from a plant community can be idiosyncratic both across species and across aspects of resource capture within a species. Thus, species identity and responses measured should be a critical consideration in future soil feedback studies.

5.4.2 Differential responses of species to soil collections

Resource capture and allocation varied similarly among grass species grown in soil from the same field plot. However, biomass responses were significantly more similar for species of like life history/provenance and somewhat more similar for closely related species, while root : shoot ratio responses were significantly more similar for closely related species. Most soil feedback studies have observed species-specific responses to soil biota from the same source (e.g., Holah and Alexander 1999, Olff et al. 2000; but see Bever 1994). Our results suggest that plant relatedness and shared origin can both influence how plants respond to communities of soil biota, refining these prior findings.

5.4.3 Plant community effects on soil feedbacks

Plant community composition had varied effects on species performance, as has previously been observed (Bartelt-Ryser et al. 2005), but our results suggest that species identity is a critical consideration when examining soil feedbacks, and that many aspects of plant community structure can contribute to soil feedbacks. Presence and increasing abundance of closely related species in the community from which soil was collected were associated with decreases in root : shoot ratio of two of the three *Bromus* spp. and increases in growth rate of *H. murinum*, suggesting that phylogenetic relatedness can influence soil feedbacks in a community setting. Different performance aspects for multiple species were affected by growth in soil collected from plots where certain species, such as *E. glaucus* and *H. murinum*, had been present, suggesting that some species may have broader effects on soil feedbacks than others. Bartelt-Ryser et al. (2005) also found that presence of certain species in an experimental community could affect several response variables of plants grown in soil from that community. Species richness in field plots was associated with decreases in growth rate of two grass species in soil from those plots, but whether this relationship is due to diversity or increased likelihood of certain species being present in richer plots is unclear. Bartelt-Ryser et al. (2005) observed some effects of plot diversity on plant responses to soil from those plots, which were often short-lived and differed among study species, but presence of legumes was generally significant and may have been more likely in their higher diversity plots. Here we have included abundance, presence, and richness as predictors to examine potential effects of phylogeny and life history/provenance and as an initial look at how community composition may affect soil feedbacks. Other components of community structure, such as assembly order and pairwise synergies, may also influence soil feedbacks and should be considered in future studies.

Plant species performance in the field (i.e., change in abundance over time) was generally not sufficient to predict performance of conspecifics grown in the same soil in the laboratory. This suggests that the feedbacks occurring between the plant and soil communities in a natural system go beyond simple intraspecific effects. Olff et al. (2000) observed positive effects of increasing abundance of conspecifics over time (5–10 years), but their study and ours are the only two to examine such effects to date.

More work is needed to evaluate the effects of temporal changes in the entire plant community on soil feedbacks, as well as to discern the relevant temporal scale at which to examine these effects.

5.4.4 Phylogeny vs. life history/provenance

Phylogeny and life history/provenance were both significantly associated with plant performance, with different aspects of plant performance varying to a greater or lesser extent for each grouping depending upon soil communities. Phylogeny explained the greatest proportion of variance for all measured aspects of plant performance, even though life history and provenance are confounded for grasses in our study system. Plant performance has been observed to vary with both phylogeny and life history/provenance (Garnier 1992, Holmes and Rice 1996, Seabloom et al. 2003b), but the role of these factors relative to each other has rarely been addressed (Garnier 1992). Our results demonstrate that phylogeny must be considered when comparing performance of species because, contrary to other observations (Holmes and Rice 1996), final plant biomass did not differ between plants of like life history/provenance and growth rate differences were relatively small. Thus, explicit consideration of phylogeny and comparisons among multiple species may be necessary to infer that observed differences in plant performance are representative of larger species groups.

Phylogeny and life history/provenance were often associated with responses of species to the presence of soil biota, soil samples from the same field plot, and a soil's source plant community. Effects of soil biota have previously been found to differ for species of different origins (Klironomos 2002, Callaway et al. 2004b), even within congeneric pairs (Agrawal et al. 2005). However, the potential role of phylogeny and life history/provenance in soil feedbacks has not previously been compared for either responses to the same soil collection or effects of closely related species in the plant community from which soil was collected. Our results provide important evidence that comparisons between native and exotic species, even when they differ in ecologically important traits, must still account for phylogeny. Future work that can examine the relative effects of phylogeny, provenance, and life history independent of each other would be a particularly beneficial addition to the soil feedbacks literature.

5.4.5 Implications for California grassland community dynamics

Our study cannot pinpoint the effects of soil feedbacks on community processes such as coexistence, invasion, and alternate stable states in the California grasslands; but the strength of the effect of soil biota on plant performance suggests that soil feedbacks deserve greater study in this system. Models of coexistence driven by soil feedbacks generally require negative effects of conspecifics relative to heterospecifics (Bever et al. 1997, Bever 2003), which we did not clearly observe. However, we did not explicitly compare conspecific- and heterospecific-cultured soil nor examine indirect effects of soil feedbacks, which may also play a significant role in community processes (Bever et al. 1997, Bever 2003). We observed a generally negative effect of soil biota on plant performance, suggesting that some exotic grasses may not have experienced complete release from belowground enemies (Beckstead and Parker 2003, Agrawal et al. 2005). This suggests that soil biota may not facilitate invasion for exotic grasses in general; however native species might experience stronger negative effects of soil biota (Klironomos 2002, Agrawal et al. 2005). Finally, we did not observe reciprocally negative effects of species in the field communities on performance of heterospecifics in the laboratory, suggesting that soil feedbacks do not play a major role in alternate stable states in this community. This conclusion is corroborated by modeling work in this system (Borer et al. 2007) and the documented ability of these native and exotic grasses to invade established communities in the experimental plots from which soil samples were collected (Seabloom et al. 2003b).

We conclude that phylogeny must be explicitly considered in any study comparing species responses to environmental factors, including soil feedbacks. For example, our results demonstrate that differences between two native species, such as *N. pulchra* and another perennial grass, can be greater than differences between native perennial and exotic annual grasses. As *N. pulchra* is arguably the most widely studied native species in the California grasslands (e.g., Shoulders 1994, Holmes and Rice 1996, Hamilton 1997b, Brown and Rice 2000, Seabloom et al. 2003b, Hawkes et al. 2005, Hawkes et al. 2006), great care must be taken when generalizing conclusions drawn from comparisons between it and exotic species to other native perennial grasses. In particular, future work that can evaluate the effects of phylogeny, provenance, and life history independently on plant–soil feedbacks would be beneficial. We also suggest that future studies continue to examine soil feedbacks in a whole-community setting, with various levels of control on community structure. We have observed the potential for species presence and abundance in the community from which soil was collected to affect soil feedbacks, and others have observed effects of soil biota to vary with different plant neighbors (Callaway et al. 2003, Callaway et al. 2004a, Bartelt-Ryser et al. 2005, Casper and Castelli 2007; but see Bever 1994). Finally, we suggest that more attention be paid to how soil-mediated effects on plant performance translate to changes in population growth rates. We have observed that soil feedbacks can differ among different aspects of plant performance and these effects cannot always be linearly extrapolated to demographic effects. For example, decreases in root : shoot ratio in certain soil samples may indicate either greater allocation to aboveground biomass, and thus potentially to reproduction (Samson and Werk 1986), or root necrosis (Bever 1994), with different implications for plant population growth.

ACKNOWLEDGEMENTS

We thank J. D. Bever for generous advice on experimental design. S. S. Parker, T. Rusca, and J. Orrock collected field soils used in the experiment. A. L. Adams, V. T. Adams, C. D. Benfield, L. C. Friedrichsen, B. A. Martin, S. M. Moore, and A. F. Timko assisted with experimental setup and data collection. G. Creager, B. A. Martin, T. Yoshida, and seasonal field crews assisted in gathering field data used in analyses.

J. C. Uyeda provided valuable assistance with phylogenetic analyses. Thanks also to the Sedgwick Reserve and University of California Natural Reserve System. E. T. Borer, C. E. Mitchell, S. M. Moore, E. C. Orling, P. L. Zarnetske, and two anonymous reviewers provided helpful comments on the manuscript. Work was funded by Andrew W. Mellon Foundation (O. J. Reichman and E. W. Seabloom) and NSF DEB 02-35624 (O. J. Reichman, J. Schimel, and E. W. Seabloom).

Table 5.1: Resource capture (top) and resource allocation (bottom) of grasses were compared for different species grown in soil collected from the same field plot.

Species	*B. hordeaceus*	*B. madritensis*	*E. glaucus*	*H. murinum*	*N. pulchra*
Resource capture					
B. carinatus	$0.20^{\dagger}$	$0.34^{\dagger}$	$0.53^{\ddagger}$**	0.27	$-0.13^{\ddagger}$
B. hordeaceus		$0.53^{\dagger\ddagger}$**	0.12	$0.45^{\ddagger}$*	0.005
B. madritensis			0.10	$0.48^{\ddagger}$*	−0.35
E. glaucus				$0.11^{\dagger}$	$0.36^{\ddagger}$
H. murinum					−0.12
Resource allocation					
B. carinatus	$0.43^{\dagger *}$	$0.41^{\dagger *}$	$0.55^{\ddagger}$**	0.31	$0.43^{\ddagger *}$
B. hordeaceus		$0.57^{\dagger\ddagger}$**	0.58**	$0.36^{\ddagger}$	0.25
B. madritensis			0.41*	$-0.04^{\ddagger}$	0.12
E. glaucus				$0.51^{\dagger *}$	$0.27^{\ddagger}$
H. murinum					0.24

Notes: Pearson product-moment correlations (r) are presented for pairwise comparisons of standardized total biomass (i.e., resource capture) and standardized root : shoot ratio (i.e., resource allocation) of grasses grown in pots containing whole-soil inoculums from the same experimental field plot. Significant differences are indicated as: * $P \leq 0.05$; ** $P \leq 0.01$. The six grass species grown consisted of three native species (*Bromus carinatus*, *Elymus glaucus*, and *Nassella pulchra*) and three exotic species (*B. hordeaceus*, *B. madritensis*, and *Hordeum murinum*) belonging to three different tribes.

†The species compared belonged to the same tribe.

‡The species compared belonged to the same life history/provenance group.

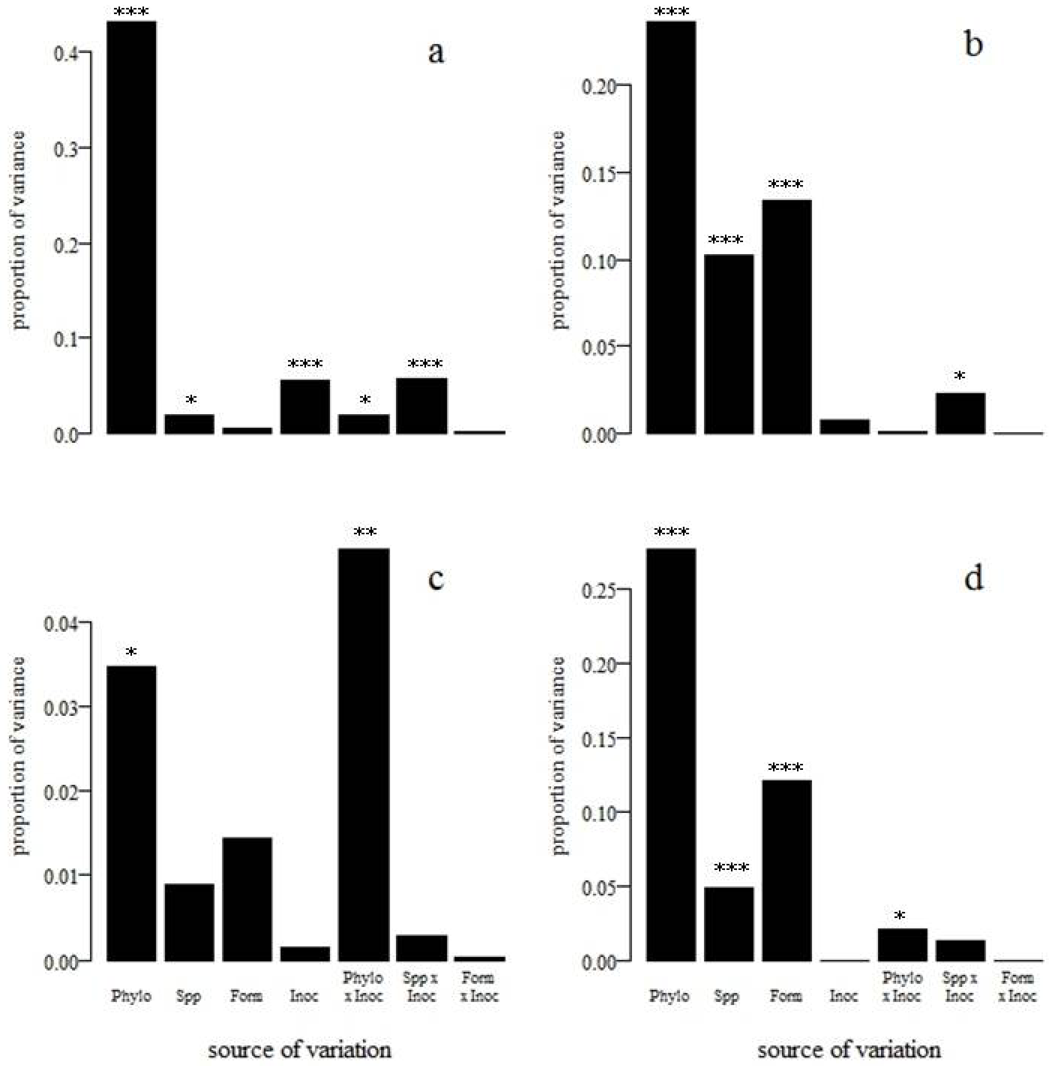

Figure 5.1: Three native perennial grass species (*Bromus carinatus*, *Elymus glaucus*, and *Nassella pulchra*) and three exotic annual grass species (*B. hordeaceus*, *B. madritensis*, and *Hordeum murinum*) comprising three tribes were grown individually in pots containing whole-soil active inocula from experimental plant communities or sterile control soil. Proportion of variance of (a) total biomass, (b) root : shoot ratio, (c) time to half of maximum height, and (d) maximum growth rate of individual grasses explained by tribe (Phylo), species nested within tribe (Spp), annual or perennial life history (Form; i.e., exotic or native, respectively), active or sterile soil (Inoc), and the first-order interactions between the three plant group factors and soil treatment are presented. Significance of each factor is indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

6 – Conclusion

My thesis examines how provenance and phylogenetic relatedness of plant species affect community dynamics and species interactions in invaded California grasslands. Both provenance and phylogeny of species can influence the ability of a species to inhabit a site and coexist with other species in the community, due to their responses to the environment and species interactions (Mitchell et al. 2006, Melbourne et al. 2007). Thus, community ecology theory can improve our understanding of the potential impacts of invasion on native biodiversity and how to mitigate those impacts by allowing us to identify the mechanisms driving recruitment limitation, physiological constraints, and species coexistence.

Heterogeneous environments can support more species than homogeneous environments, thus environmental variability may increase invasion success while lessening the probability of native species extinction (Chesson 2000, Melbourne et al. 2007). In Chapter 2, I used two California grassland data sets, one spanning 7 years at three reserves along a 500-km latitudinal gradient and one spanning 48 years at 11 sites within a single 1000-ha reserve, to determine how environmental heterogeneity in space and time contribute to variability in provenance group (i.e., native and exotic) abundance and diversity, and whether native and exotic species respond similarly to spatial and temporal variability. Temporal environmental heterogeneity appears to be the primary determinant of provenance group abundance, while spatial and temporal environmental heterogeneity both contribute to community diversity. Spatial and temporal heterogeneity must therefore be considered simultaneously when examining community dynamics and species coexistence. Provenance was a poor general predictor of species response; native and exotic species exhibit similar spatio-temporal patterns in some cases but not others. Plant persistence may thus depend more upon the abiotic environment than competition from the other provenance group as native and exotic diversity were generally positively correlated.

Whether invasion by exotic species will increase or decrease biodiversity can vary with spatial scale (Sax et al. 2002, Davis 2003), and understanding the mechanisms driving changes in local populations is important to overall species persistence (Hanski et al. 1996). Plant recruitment is limited by a combination of propagule-limitation and establishment-limitation processes, the roles of which can be evaluated through seed addition experiments (Clark et al. 2007). In Chapter 3, I used my long-term data set at one California grassland site to determine temporal changes in populations of certain native annual forbs and the roles of propagule- and establishment-limitation processes on these species' recruitment. Grassland communities appear to be exhibiting long-term transience centuries after exotic plant invasion (Hamilton 1997a, Mensing and Byrne 1998) and decades after livestock grazing ceased. A combination of propagule- and establishment-limitation processes appear to be impacting recruitment of these native annual forbs, which likely explains the declining abundances and extinction of local populations observed over the course of monitoring. Extinction of local populations and enhanced recruitment in sites with documented species occupancy suggest that maintenance of documented populations is critical to long-term species persistence (Hanski et al. 1996). Build-up of plant litter appears to be the primary mechanism by which exotic grasses limit recruitment of native forbs (Hayes and Holl 2003a, Coleman and Levine 2007), but a site's grazing history and community composition can influence the effects of grass competition on recruitment.

Recruitment to communities through dispersal and establishment processes determines community diversity (Keddy 1992, Weiher and Keddy 1995), and disturbance and resource supply can either increase or decrease diversity through their effects on mechanisms of community assembly (Petraitis et al. 1989, Foster and Gross 1998, Chase 2007, Hillebrand et al. 2007, Chase 2010). As I show in Chapter 4, disturbance that involves removal of plant litter can increase recruitment of native annual forbs, a diverse component of the California grasslands flora. Expanding the scope of "diversity" to include species' evolutionary history (phylogenetic relationships) can improve our understanding and predictions of community assembly if phylogeny correlates with ecological similarity (Webb et al. 2002, Cavender-Bares et al. 2009). In Chapter 4, I examined the effects of disturbance and nitrogen supply on local community diversity and variation in community composition across the region. Disturbance increased diversity and variability among communities, likely through increased opportunities for colonization. Nitrogen supply had less of an effect, though it did alter community composition and interact with disturbance to lower diversity. In general, these grassland communities may be structured more by environmental filtering than other assembly processes, where resident communities limit colonization by additional species (Webb et al. 2002, Chase 2007, Seabloom 2011). Incorporating phylogenetic relationships to provide insight into mechanisms structuring communities is only useful if those relationships correspond to traits on which these mechanisms might act (Cavender-Bares et al. 2009). Exploring the roles of additional biotic interactions that may structure communities would further elucidate the mechanisms governing diversity.

Plant–soil feedbacks can affect plant community dynamics by influencing processes of coexistence or invasion, or by maintaining alternate stable states (Bever et al. 1997, Bever 2003, Mitchell et al. 2006, Van der Putten et al. 2007). Phylogenetic relatedness may be a critical factor governing such feedbacks in invaded communities because exotics more closely related to natives may be more likely to gain soil pathogens and/or mutualists in their introduced range (Richardson et al. 2000, Agrawal et al. 2005, Mitchell et al. 2006). In Chapter 5, I examined the effects of soil biota from experimentally established native and invaded California grassland communities on performance of three native and three exotic grasses, comprising three tribes. Phylogeny was the greatest determinant of most aspects of performance, but soil biota also had an effect on resource capture (i.e., total plant biomass). Provenance was a good predictor of a plant's biomass response to a soil community, while phylogeny was better at predicting the resource allocation response (i.e., root : shoot ratio). Thus, both phylogeny and provenance can predict species performance and responses to biotic interactions, though they may affect different aspects of performance.

Here I have examined community dynamics and species interactions in the invaded California grasslands to explore the roles of provenance and phylogeny on species interactions, recruitment, and community structure, ultimately to provide insight on coexistence of native species in this exotic-dominated landscape. I have shown that native and exotic species abundance and diversity is highly variable in both time and space, but these provenance group responses are rarely negatively correlated (Chapter 2). Thus, exotic species do not appear to exclude natives as a whole from communities. Long-term abundance patterns further suggest that the system remains in a state of transience, and populations of several native species are declining at local scales (Chapter 3). Recruitment limitation due to the build-up of plant litter associated with exotic grasses may be generally responsible for these declines, but habitat suitability, land-use history, and community composition also affect native recruitment. Across the grasslands, disturbance and resource supply can interact to affect both species and phylogenetic diversity (Chapter 4). Disturbance in particular can increase diversity, likely by increasing opportunities for colonization by removing plant litter that previously limited recruitment. Both phylogeny and provenance can also affect biotic interactions, such as with communities of soil organisms (Chapter 5). Thus, I have shown that spatio-temporal heterogeneity, alterations to the biotic environment mediated by exotic invasion, and phylogenetic relationships among species are all important considerations when evaluating impacts of invasion and designing management strategies to conserve native biodiversity, especially in light of anthropogenic influence on disturbance regimes and resource supply.

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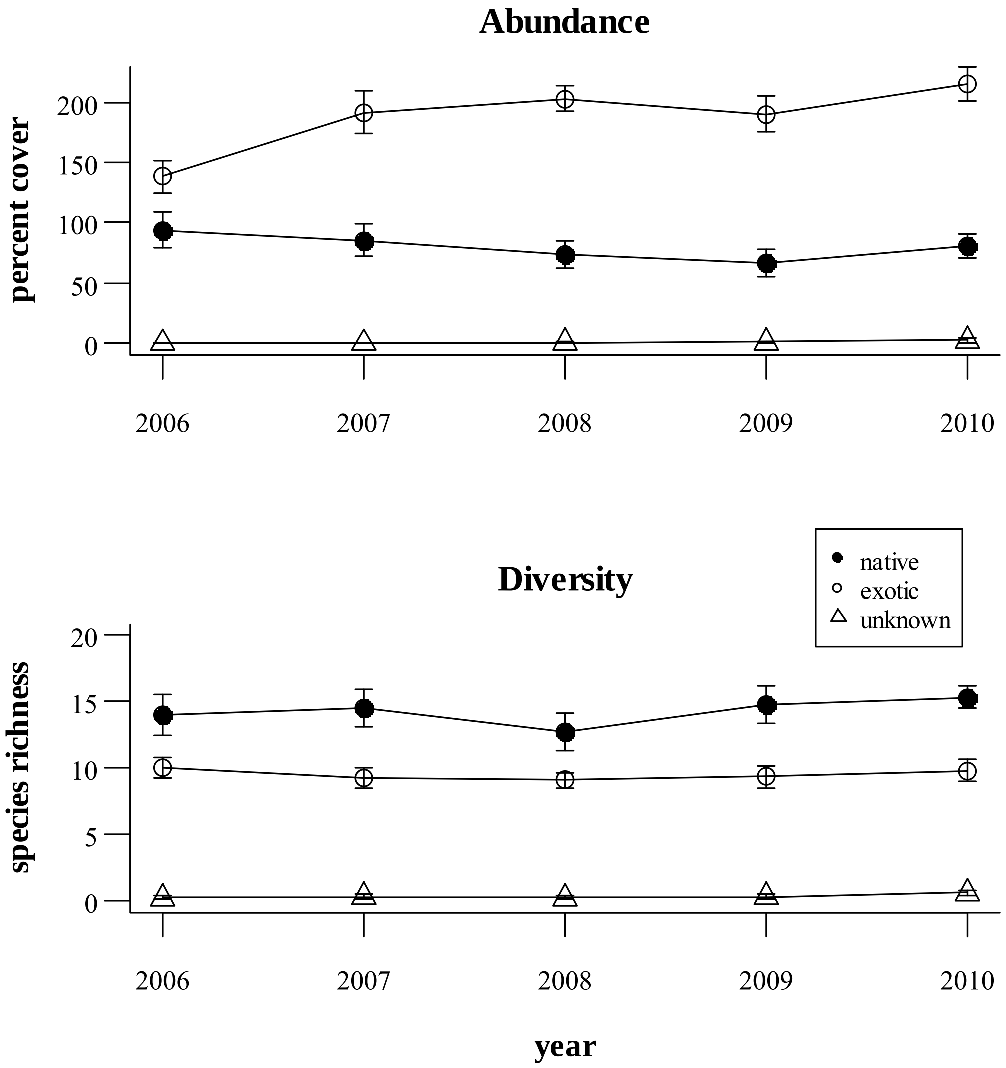
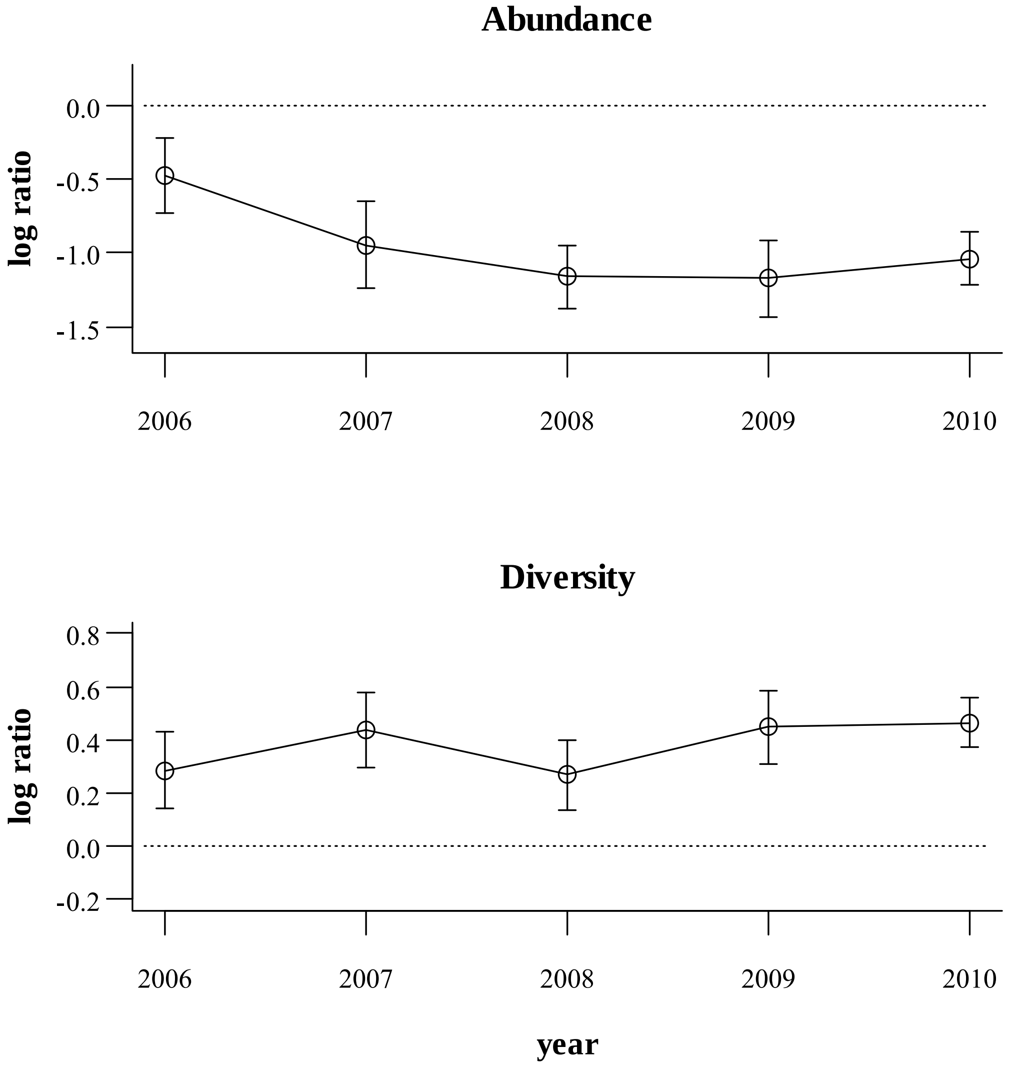
APPENDICES

Appendix A



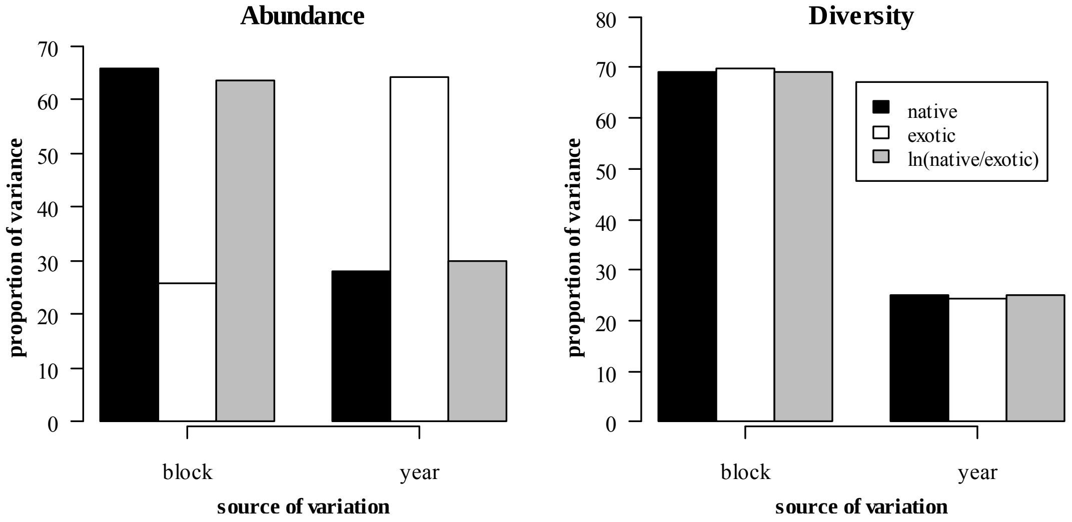
Appendix A: Abundance (top) and diversity (bottom) of native, exotic, and unclassifiable plants in 11 California grassland blocks at the Hastings Natural History Reservation sampled for 5 years. Abundance was estimated as the summed percent cover of native, exotic, or unclassifiable plants in three ½×1-m quadrats located at each end and the center of a 40-m transect. Diversity was estimated as the total richness of native, exotic, and unclassifiable species in all three quadrats combined. Values presented are means ± SE, thus error bars represent within-site variability in responses.

Appendix B



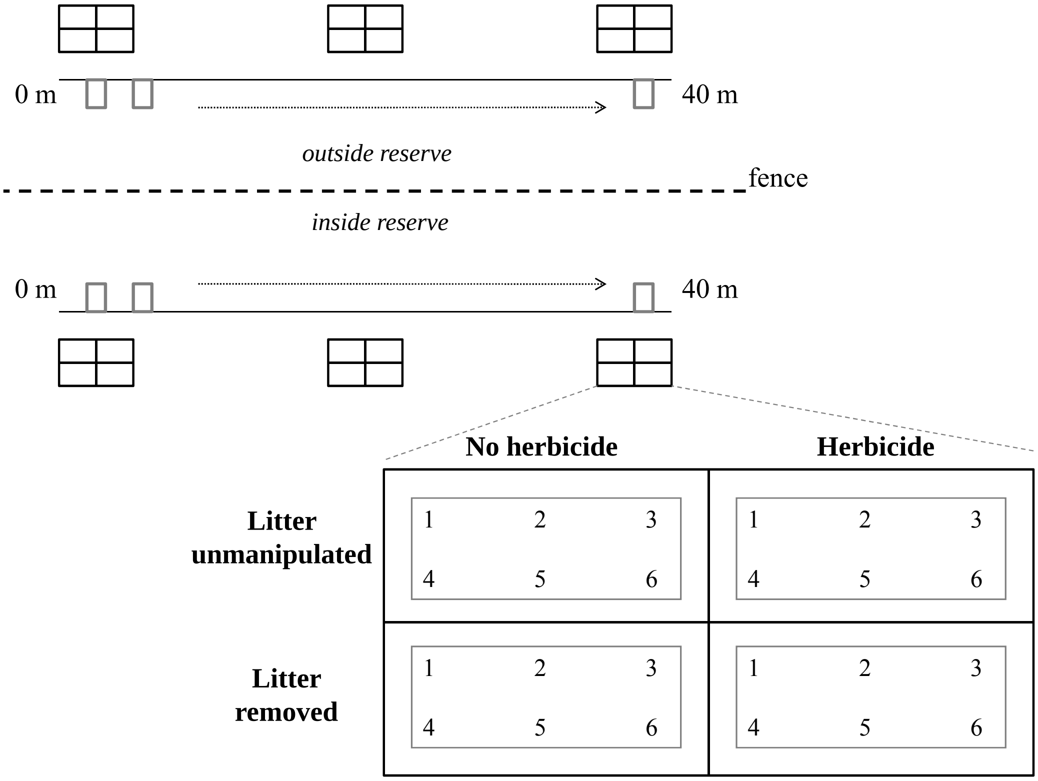
Appendix B: Ratios of native to exotic abundance (top) and diversity (bottom) in 11 California grassland blocks at the Hastings Natural History Reservation sampled for 5 years. Ratios were calculated as ln(native response / exotic response) for each block's native and exotic plant abundance and diversity, estimated as percent cover and richness, respectively. Negative values (below dotted lines) indicate the native response was less than the exotic response.

Appendix C



Appendix C: Proportion of variation in abundance (left) and diversity (right) of native and exotic plants and log ratios of native to exotic abundance and diversity accounted for by nested spatial (block) and temporal (year) variables. Data were collected from 11 blocks within the Hastings Natural History Reservation over 5 years. Abundance was estimated as the summed percent cover of native or exotic plants in three ½×1-m quadrats located at each end and the center of a 40-m transect. Diversity was estimated as the total richness of native or exotic species in all three quadrats combined. Ratios were calculated as ln(native response / exotic response) for each block's native and exotic plant abundance and diversity.

Appendix D



Appendix D: Nested experimental design where three blocks of treatment plots were established at the ends and middle of paired monitoring transects located inside and outside the Hastings Natural History Reservation boundary at 11 sites. Each block consisted of four plots in a two-way factorial design of litter removal and herbicide application to remove live grass. A cover quadrat was located in the center of each treatment plot and six native annual forb species were seeded into each quadrat at one species per grid location.

Appendix E

Appendix E: Effect sizes and significance of predictors included in a statistical mixed effects model describing temporal trends in abundance of six native annual forbs within transects located inside and outside the reserve boundary of the Hastings Natural History Reservation over 48 years. The model included nested random effects of sampling year within transect on a side of the reserve boundary within site. The model was rerun with each species as the reference factor to determine pairwise interactions in temporal trends among species; significantly different pairwise comparisons are listed.
† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$

	Predictors						
Species	Year	Inside boundary	Year X boundary	Mean abundance of other species	Year X other species	Boundary X other species	Year X boundary X other species
CAEX	-0.001*	-4.38†	0.002†	CLPU**, COHE*, TRMI**	CLPU**, COHE*, TRMI**	CLPU†	CLPU†
CLPU	0.002**	0.42	-0.0002	CAEX**, PLER**	CAEX**, PLER**	CAEX†, COHE**	CAEX†, COHE**
COHE	0.001	-8.70**	0.004**	CAEX*, PLER*	CAEX*, PLER*	CLPU**, NEME*, PLER*, TRMI*	CLPU**, NEME*, PLER*, TRMI**
NEME	0.0002	0.21	-0.0001	*None significant*	*None significant*	COHE*	COHE*
PLER	-0.002*	-0.89	0.0004	CLPU**, COHE*, TRMI**	CLPU**, COHE*, TRMI**	COHE*	COHE*
TRMI	0.002**	-0.32	0.0002	CAEX**, PLER**	CAEX**, PLER**	COHE*	COHE**

Appendix F

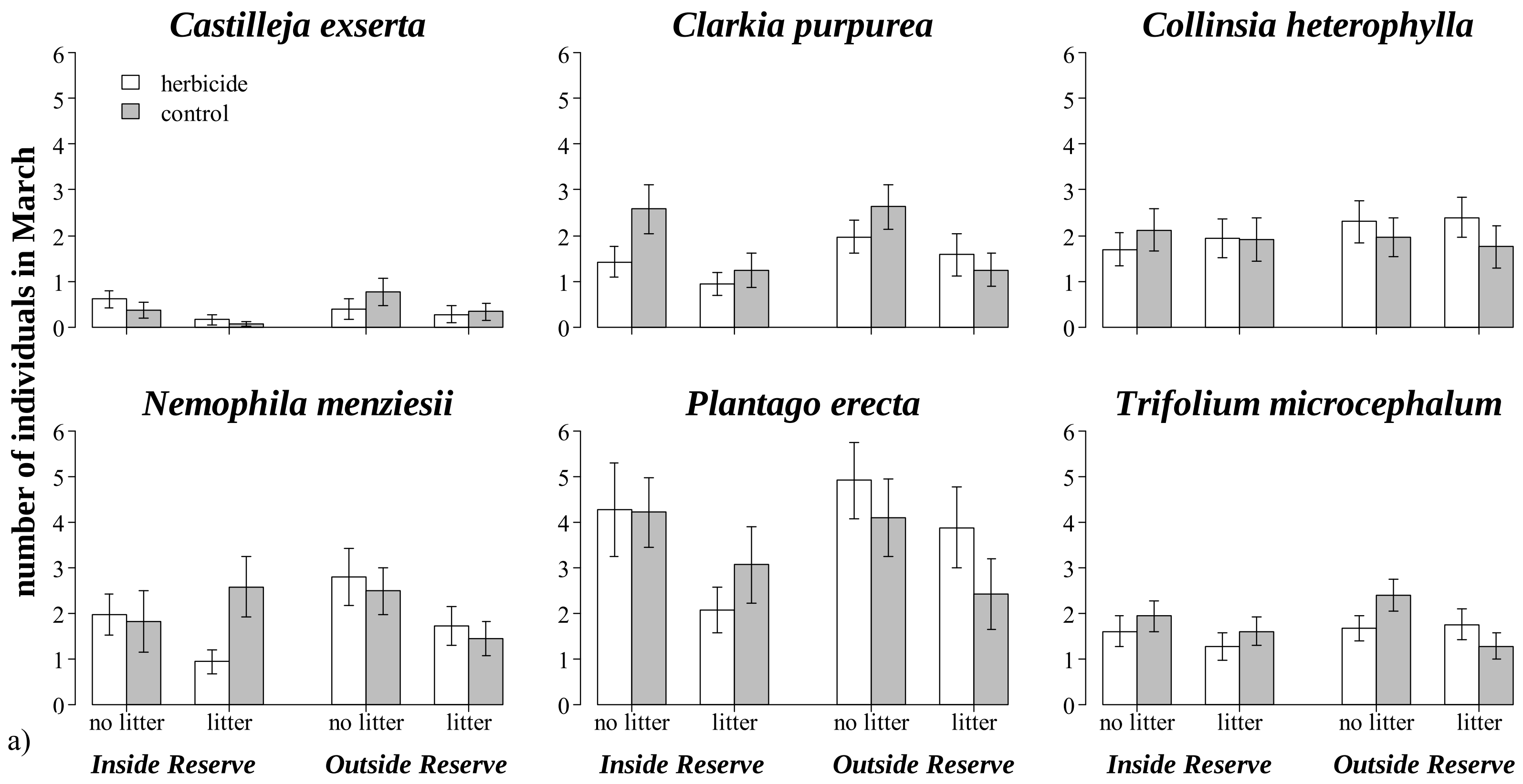
Appendix F: Effect sizes and significance of predictors included in statistical mixed effects models describing recruitment of six native annual forb species seeded into competition removal plots located inside and outside the reserve boundary of the Hastings Natural History Reservation. Each model included nested random effects of sampling date within experimental block within side of reserve boundary within site. Seven models were examined: one for each species and one for the total recruitment of all seeded species per plot.
† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *NA* indicates the predictor was not included in the final model

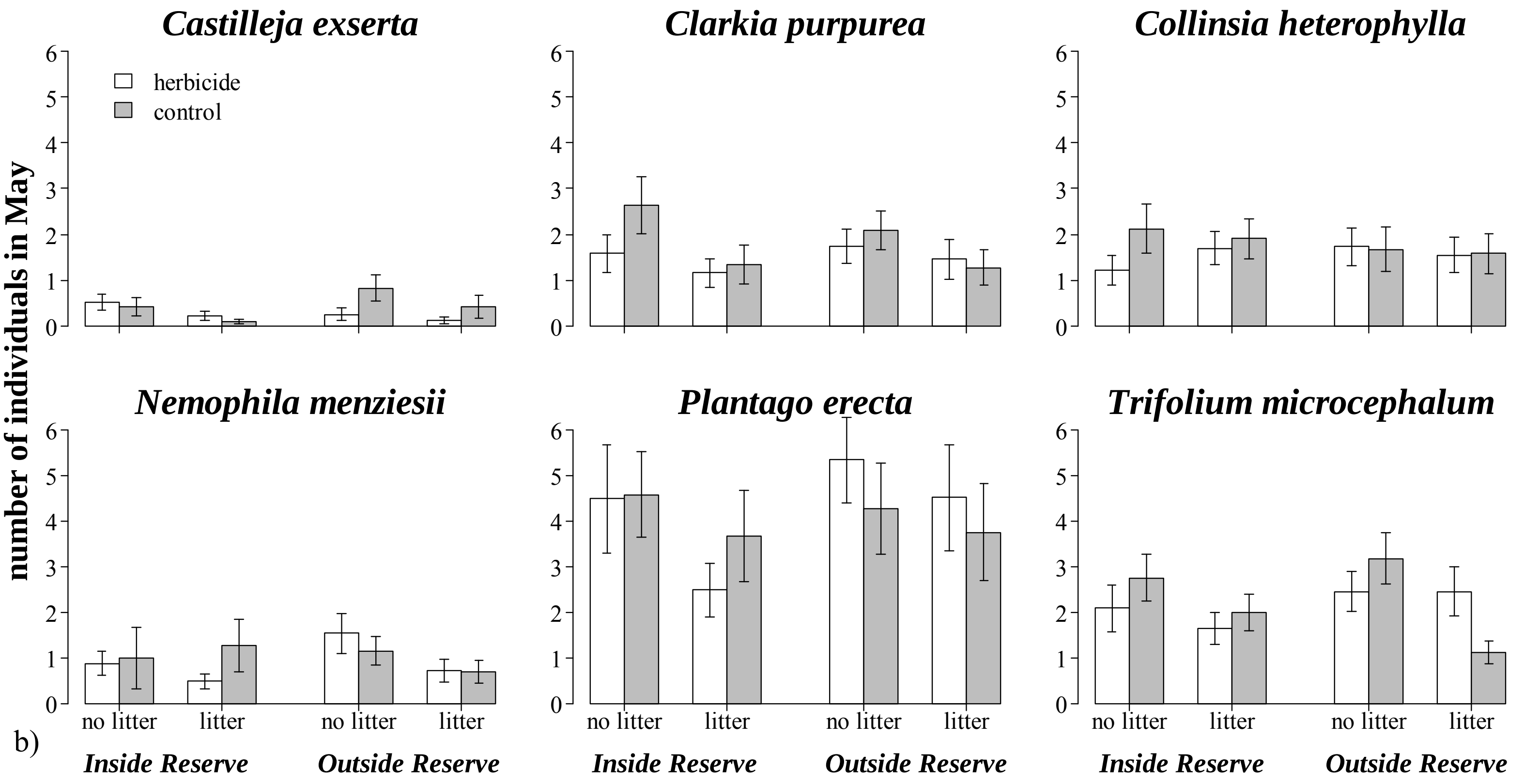
	Predictors						
Species	Litter present	Live-grass present	Inside boundary	Litter X live-grass	Litter X boundary	Live-grass X boundary	Litter X live-grass X boundary
Total recruitment	−0.16**	0.11†	−0.13	−0.29**	−0.23**	0.16*	0.41**
CAEX	−0.48*	1.00**	0.43	NA	−0.89*	−1.15**	*NA*
CLPU	−0.23*	0.15	−0.33	−0.45**	*NA*	0.43**	*NA*
COHE	0.15	−0.06	*NA*	−0.32*	*NA*	*NA*	*NA*
NEME	−0.53**	0.31†	−0.66*	0.13	−0.22	0.12	0.83**
PLER	−0.20*	−0.20*	0.04	−0.10	−0.46**	0.21†	0.49**
TRMI	0.11	0.25†	−0.21	−0.95**	−0.32†	−0.02	0.84**

Species	Predictors (continued)							
	Never observed vs present	Gone extinct vs not	Stable presence vs colonizing	Mean observed abundance	Litter mass	Total forb cover	Exotic forb cover	Total grass cover
Total recruitment	*NA*	*NA*	*NA*	*NA*	−0.002*	0.007**	−0.005*	*NA*
CAEX	−0.58*	−0.67†	*NA*	−13.30	−0.002	0.03**	−0.02*	*NA*
CLPU	*NA*	*NA*	*NA*	*NA*	*NA*	0.008*	−0.02**	*NA*
COHE	−0.72*	*NA*	*NA*	*NA*	−0.003*	0.01**	*NA*	0.02**
NEME	−0.06	0.22	1.46**	*NA*	*NA*	0.007*	−0.006	−0.01**
PLER	−0.25*	−0.18	*NA*	*NA*	−0.004**	*NA*	*NA*	*NA*
TRMI	*NA*	*NA*	*NA*	*NA*	*NA*	0.01**	−0.01**	0.006†

Note: “Litter present” and “live grass present” refer to competition removal treatments of plant litter removal and grass-specific herbicide, respectively, applied to plots in a factorial design. “Inside boundary” refers to plot location inside the reserve boundary vs. outside it. “Never observed vs. present”, “gone extinct vs. not”, and “stable presence vs. colonizing” refers to orthogonal contrasts of recruitment conducted based on each species’ occupancy of a transect during long-term monitoring (see Table 3.1). “Mean observed abundance” refers to a species’ overall mean abundance in a transect documented during long-term monitoring. “Litter mass” refers to the mean mass of plant litter removed from the two litter removal plots within each experimental block. “Total forb cover”, “exotic forb cover”, and “total grass cover” refer to visually estimated cover of each plant group in each plot in May 2010.

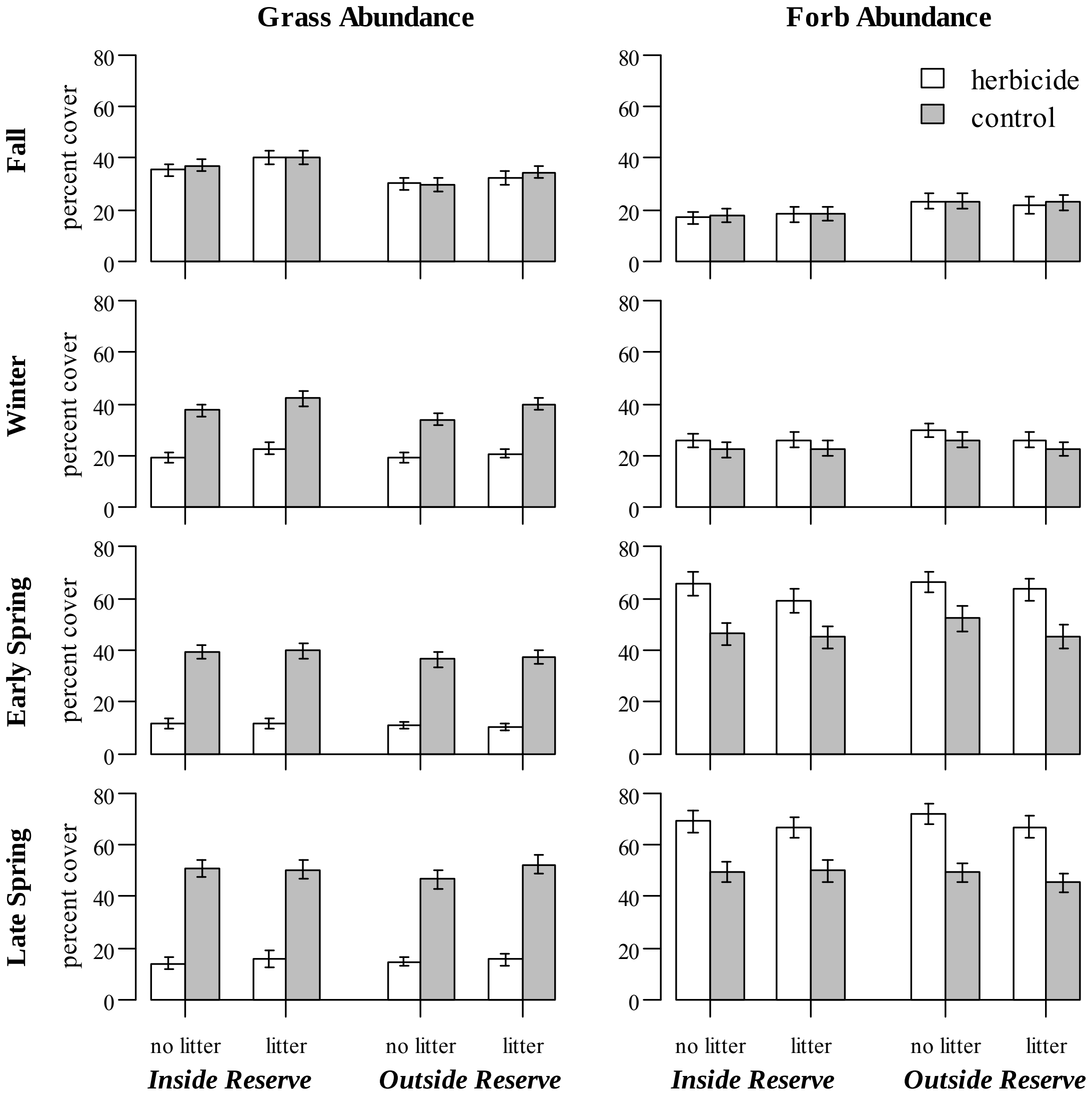
Appendix G


Castilleja exserta
Clarkia purpurea
Collinsia heterophylla
Nemophila menziesii
Plantago erecta
Trifolium microcephalum
□ herbicide
▨ control
number of individuals in March
0
1
2
3
4
5
6
no litter
litter
no litter
litter
Inside Reserve
Outside Reserve
a)



Appendix G: Recruitment per plot of six native annual forb species recorded in (a) March and (b) May. Seeds for each species were seeded into competition removal plots located along long-term monitoring transects inside and outside the Hastings Natural History Reservation boundary. Litter removal and grass-specific herbicide treatments were applied to plots in a factorial design.

Appendix H



Appendix H: Total grass and forb cover in competition removal plots located along long-term monitoring transects inside and outside the Hastings Natural History Reservation boundary. Litter removal and grass-specific herbicide treatments were applied to plots in a factorial design. Cover was visually estimated four times over the course of the growing season: fall (October-November 2009), winter (December 2009), early spring (March 2010), and late spring (May 2010).

Appendix I

Appendix I: List of species included in the phylogeny, with GenBank accession numbers for gene sequences that were available. If a congener, contribal, or confamilial species was used, it is listed as a “congener”. Species added to the phylogeny as outgroup species or to help resolve clades with few species are indicated as “added”. Species added to the phylogeny as polytomies with their closest relatives are included in the table but have no accession numbers.

Species	Family	*rbcl*	*matk*	*ITS1*	5.8s	*ITS2*	Congener	Added
AGOSERIS GRANDIFLORA	Asteraceae			AF386493	AF386493	AF386493		
AGOSERIS HETEROPHYLLA	Asteraceae			L13954	L13954	L13954		
AIRA CARYOPHYLLEA	Poaceae	AM849361	DQ786878	AM049252	AM049252	AM049252		
ALLIUM CRISPUM	Alliaceae	Z69205		AF055106	AF055106	AF055106	Allium subhirsutum	
AMBORELLA TRICHOPODA	Amborellaceae	L12628	AF465284					yes
AMSINCKIA MENZIESII	Boraginaceae		AY092894	AY092901	AY092901	AY092901	Eritrichium nanum	
ANAGALLIS ARVENSIS	Primulaceae	M88343		EF436994	EF436994	EF436994		
ANAGALLIS FOEMINA	Primulaceae			DQ256370	DQ256370	DQ256370		yes
APIUM GRAVEOLENS	Apiaceae	L01885	AJ429370	GQ379288	GQ379288	GQ379288		yes
ASTERACEAE SPECIES	Asteraceae							

ASTRAGALUS GAMBELIANUS	Fabaceae			AF121709	AF121709	AF121709	Astragalus douglasii
ATHYSANUS PUSILLUS	Brassicaceae			EF514629	EF514629	EF514629	
AVENA BARBATA	Poaceae			DQ995454	DQ995454	DQ995454	
AVENA FATUA	Poaceae	AJ746257		DQ995473	DQ995473	DQ995473	
BACCHARIS PILULARIS	Asteraceae	EU384949	EU385326	U97604	U97604	U97604	Baccharis neglecta
BLOOMERIA CROCEA	Alliaceae	Z69214					
BRASSICA NIGRA	Brassicaceae		AB354272	EF601911	EF601911	EF601911	
BRASSICACEAE SPECIES	Brassicaceae						
BRIZA MINOR	Poaceae		DQ786892	EU935584	EU935584	EU935584	
BRODIAEA SPECIES	Themidaceae	AF116993					Brodiaea jolonensis
BROMUS ARENARIUS	Poaceae	AY691632		U83370		U83371	
BROMUS CARINATUS	Poaceae			AY367948	AY367948	AY367948	
BROMUS DIANDRUS	Poaceae			AY367936	AY367936	EU036204	
BROMUS HORDEACEUS	Poaceae	AY395531	GQ248088	AF494347	AF494347	AF494347	
BROMUS LAEVIPES	Poaceae			AY367917	AY367917	AY367917	
BROMUS MADRITENSIS	Poaceae			EU036195		EU036205	
BROMUS TECTORUM	Poaceae	GQ373395		AJ608154	AJ608154	AJ608154	

CALANDRINIA CILIATA	Portulacaceae		AY764127	L78021	L78021	L78021		
CALOCHORTUS LUTEUS	Liliaceae	AY465704					Calochortus apiculatus	
CALYCADENIA PAUCIFLORA	Asteraceae			EU853462	EU853462	EU853462	Layia hieracioides	
CALYSTEGIA PURPURATA	Convolvulaceae	AY100992	FJ395438	AY560267	AY560267	AY633667	Calystegia sepium	
CAPSELLA BURSA-PASTORIS	Brassicaceae	DQ310539	NC_009270	AF055196	AF055196	AF055196		
CASTILLEJA DENSIFLORA	Orobanchaceae			EF103689	EF103689	EF103689		
CASTILLEJA EXSERTA	Orobanchaceae			EF103688	EF103688	EF103688		
CENTAUREA MELITENSIS	Asteraceae	EU384954	EU385332	DQ319132	DQ319132	DQ319132		
CENTAURIUM MUEHLENBERGII	Gentianaceae			AY047785		AY047863		
CERASTIUM ARVENSE	Caryophyllaceae		AY936295					
CERASTIUM FONTANUM	Caryophyllaceae	FJ395574	AY936296	AY936241	AY936241	AY936241		yes
CERASTIUM GLOMERATUM	Caryophyllaceae	M83542		AY857977	AY857977	AY857977		
CIRSIUM OCCIDENTALE	Asteraceae			AF443702	AF443702	AF443702		
CIRSIUM SPECIES	Asteraceae							
CIRSIUM VULGARE	Asteraceae			AF443716	AF443716	AF443716		

CLARKIA PURPUREA	Onagraceae			AY271531	AY271531	AY271531	Clarkia pulchella	
CLARKIA UNGUICULATA	Onagraceae			EF017402	EF017402	EF017402		
CLAYTONIA PERFOLIATA	Portulacaceae	AF132093	AY764091	AY764040	AY764040	AY764040		
CONVOLVULUS ARVENSIS	Convolvulaceae	AY100993	FJ395388	AY560274	AY560274	AY560274		yes
CONYZA CANADENSIS	Asteraceae			AY875694	AY875694	AY875694		
CORETHROGYNE FILAGINIFOLIA	Asteraceae			U97618	U97618	U97618		
CROTON ALABAMENSIS	Euphorbiaceae	EF405831	EF135523	AY971177	AY971177	AY971177		yes
CROTON LUNDELLII	Euphorbiaceae	EF405844		DQ227527	DQ227527	DQ227527		yes
CYNOSURUS ECHINATUS	Poaceae			AF532937	AF532937	AF532937		
DAUCUS PUSILLUS	Apiaceae			AF077788	AF077788	AF077103		
DICHELOSTEMMA CAPITATUM	Themidaceae			EU096190	EU096190	EU096190		
DICHELOSTEMMA MULTIFLORUM	Themidaceae	Z69211		EU096193	EU096193	EU096193		yes
DODECATHEON CLEVELANDII	Primulaceae		AY647467					
DODECATHEON REDOLENS	Primulaceae		AY647477	EU887001	EU887001	EU887001		yes
DRABA VERNA	Brassicaceae			AY047686	AY047686	AY047686		

ELYMUS GLAUCUS	Poaceae			FJ040161	FJ040161	FJ040161	
EMMENANTHE PENDULIFLORA	Hydrophyllaceae			AF091158	AF091158	AF091158	
EPILOBIUM SPECIES1	Onagraceae			L28015	L28015	L28015	Epilobium ciliatum
EPILOBIUM SPECIES2	Onagraceae			L28019	L28019	L28019	Epilobium densiflorum
EREMOCARPUS SETIGERUS	Euphorbiaceae	EF405853		AY971249	AY971249	AY971249	
ERODIUM BOTRYS	Geraniaceae			EF185365	EF185365	EF185365	
ERODIUM CICUTARIUM	Geraniaceae	DQ452882	AM396500	EF185393	EF185393	EF185393	
ERYSIMUM SPECIES	Brassicaceae	AY167980		AY254534	AY254534	AY254534	Erysimum capitatum
ESCHSCHOLZIA CAESPITOSA	Papaveraceae						
ESCHSCHOLZIA CALIFORNICA	Papaveraceae	U86625	GU266597	DQ912883	DQ912883	DQ912883	
EUPHORBIA CRENULATA	Euphorbiaceae	AY794819		GU214943	GU214943	GU214943	Euphorbia pulcherrima
EUPHORBIA SPATHULATA	Euphorbiaceae	AB233884	AB233780	EU659774	EU659774	EU659774	Euphorbia humifusa
FILAGO CALIFORNICA	Asteraceae	GQ436476		EF108400	EF108400	EF108400	Gnaphalium affine
FILAGO GALLICA	Asteraceae			AY445231	AY445231	AY445231	Filago pyramidata
FRITILLARIA SPECIES	Liliaceae	GQ248610	AY624427	AY616710	AY616710	AY616710	Fritillaria affinis

GALIUM ANDREWSII	Rubiaceae	X81102					Galium parisiense	
GALIUM APARINE	Rubiaceae	X81091		AF419175	AF419175	AF419192		
GASTRIDIUM VENTRICOSUM	Poaceae		DQ786914	DQ336817	DQ336817	DQ336817		
GERANIUM DISSECTUM	Geraniaceae		FJ395400	AY944413	AY944413	AY944413		
GILIA ACHILLEIFOLIA	Polemoniaceae		L34175	AF006097	AF006097	AF006097		
GILIA CAPITATA	Polemoniaceae		L34182	AF006110	AF006110	EU339740		
GILIA CLIVORUM	Polemoniaceae			AF202935	AF202935	AF202935		
GILIA TRICOLOR	Polemoniaceae			AF006119	AF006119	AF006119		
GITHOPSIS PULCHELLA	Campanulaceae	EU713420	EU713313					yes
GITHOPSIS SPECULARIOIDES	Campanulaceae	EU713417	EU713310	AY322056		AY331469	Githopsis diffusa	
HAZARDIA SQUARROSA	Asteraceae			U97613	U97613	U97613		
HEMIZONIA FASCICULATA	Asteraceae			AF494350	AF494350	AF229322	Hemizonia congesta	
HESPEREVAX SPECIES	Asteraceae	AB530970	AF318919				Rhodanthe manglesii	
HOLOCARPHA VIRGATA	Asteraceae			AF229321	AF229321	AF229321		
HORDEUM MURINUM	Poaceae	AY836172	AB078120	AJ607990	AJ607990	AJ607990		
HYPOCHAERIS GLABRA	Asteraceae		AJ633232	AY504692	AY504692	AY504692		
JATROPHA INTEGERRIMA	Euphorbiaceae	AY794902	AB233775	AY971261	AY971261	AY971261		yes

JUNCUS AMBIGUUS	Juncaceae	AY216612	AY973527	AY727794	AY727794	AY727794	Juncus effusus
JUNCUS BUFONIUS	Juncaceae	AY216615		AY727789	AY727789	AY727789	
LACTUCA SERRIOLA	Asteraceae		AJ633237	AJ633332	AJ633332	AJ633332	
LACTUCEAE SPECIES1	Asteraceae						
LACTUCEAE SPECIES2	Asteraceae			AY218988	AY218988	AY218988	Malacothrix clevelandii
LAGOPHYLLA RAMOSISSIMA	Asteraceae			AF229310	AF229310	AF229310	
LAMARCKIA AUREA	Poaceae	AJ784834		AF532936	AF532936	AF532936	
LATHYRUS ANGULATUS	Fabaceae			AY839343	AY839343	AY839343	
LEPIDIUM NITIDUM	Brassicaceae		DQ406766	EF368007	EF368007	EF368007	Lepidium perfoliatum
LINANTHUS BICOLOR	Polemoniaceae		AF120118	AF264725	AF264725	AF264725	
LINANTHUS CILIATUS	Polemoniaceae		AF120124	AF067546	AF067546	AF067546	
LINANTHUS PARVIFLORUS	Polemoniaceae		AF120121	AF264728	AF264728	AF264728	
LINANTHUS PYGMAEUS	Polemoniaceae		AF120136	AF119438		AF119464	
LOLIUM MULTIFLORUM	Poaceae			AJ240141	AJ240141	AF532946	
LOLIUM PERENNE	Poaceae	AY395547	DQ786925	AF303401	AF303401	AF303401	

LOLIUM TEMULENTUM	Poaceae			AJ240145	AJ240145	AJ240145		
LOMATIUM UTRICULATUM	Apiaceae			U30580		U30581	Lomatium dasycarpum	
LOTUS HUMISTRATUS	Fabaceae			DQ641988	DQ641988	DQ641988		
LOTUS PURSHIANUS	Fabaceae		AF142729	AF467067	AF467067	AF467067		
LOTUS SCOPARIUS	Fabaceae			AF218521	AF218521	AF218521		
LOTUS STRIGOSUS	Fabaceae			AF218513	AF218513	AF218513		
LOTUS WRANGELIANUS	Fabaceae			AF218514	AF218514	AF218514		
LUPINUS NANUS	Fabaceae	Z70056		Z72176	AY338928	AF007441		
LUPINUS SUCCULENTUS	Fabaceae			AF007494	AF007494	AF007494		
MADIA ELEGANS	Asteraceae			AF413612	AF413612	AF413612		
MADIA GRACILIS	Asteraceae			EU853464	EU853464	EU853464	Madia sativa	
MADIA MADIOIDES	Asteraceae			AF061914	AF061914	AF061914		
MAGNOLIA GRANDIFLORA	Magnoliaceae	AF119180	AM889723					yes
MEDICAGO POLYMORPHA	Fabaceae		AF522104	DQ311981	DQ311981	DQ311981		
MELICA SPECIES	Poaceae		AM234580	FM179418	FM179418	FM179418	Melica picta	
MIMULUS AURANTIACUS	Phrymaceae	AF026835	AY849605	AY575390	AY575390	AY575390		yes
MIMULUS SPECIES	Phrymaceae		AY667471	AY575439	AY575439	AY575439	Mimulus guttatus	

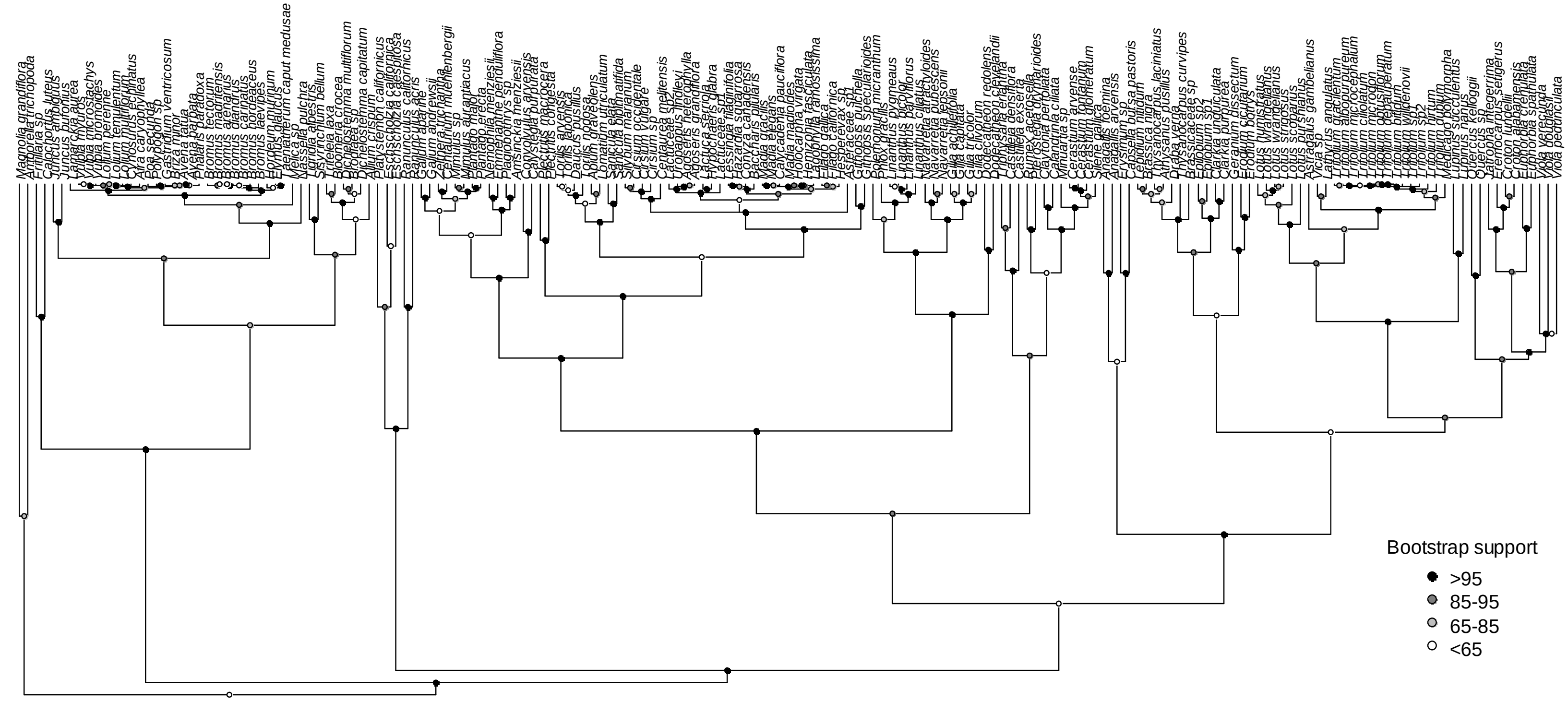
MINUARTIA SPECIES	Caryophyllaceae		AY936316	AY857970	AY857970	AY936263	Minuartia graminifolia	
NASSELLA PULCHRA	Poaceae	EF125159		AF529227	AF529227	AF529227	Nassella trichotoma	
NAVARRETIA ATRACTYLOIDES	Polemoniaceae			U73861	U73861	U73861		
NAVARRETIA JEPSONII	Polemoniaceae		EU628545	U73877	U73877	U73877		
NAVARRETIA PUBESCENS	Polemoniaceae		EU628546	U73879	U73879	U73879		
NEMOPHILA MENZIESII	Hydrophyllaceae			AF091183	AF091183	AF091183		
PHALARIS PARADOXA	Poaceae	AJ784827	AF164396				Phalaris arundinacea	
PHLOX GRACILIS	Polemoniaceae		L34203	AF067553	AF067553	AF067553		
PLAGIOBOTHRYS SPECIES	Boraginaceae		AY092896	AY092899	AY092899	AY092899	Plagiobothrys albiflorus	
PLANTAGO ERECTA	Plantaginaceae			AY101909	AY101909	AY101909		
PLANTAGO MAJOR	Plantaginaceae	GQ248674	GQ248180	AB281165	AB281165	AB281165		yes
PLATYSTEMON CALIFORNICUS	Papaveraceae	U86630		AF305339		AF305349		
PLECTRITIS CONGESTA	Valerianaceae		AY310486	AY792827	AY792827	AY792827		
PLECTRITIS MACROCERA	Valerianaceae	AF446955	AF446925	AY236195	AY236195	AY236195		yes
POA SECUNDA	Poaceae			EU792393	EU792393	EU792393		

POLEMONIUM MICRANTHUM	Polemoniaceae		EU628513	DQ320791	DQ320791	DQ320791		
POLYPOGON SPECIES	Poaceae		AM234719	DQ146795	DQ146795	DQ146795	Polypogon monspeliensis	
PTEROSTEGIA DRYMARIOIDES	Polygonaceae	GQ206229	GQ206206	GQ206263	GQ206263	GQ206263		
QUERCUS AGRIFOLIA	Fagaceae			AF098415	AF098415	AF098415		
QUERCUS KELLOGGII	Fagaceae			AF098416	AF098416	AF098416		yes
RANUNCULUS ACRIS	Ranunculaceae	AY395557	AY954199	FM242806	FM242806	FM242806		yes
RANUNCULUS CALIFORNICUS	Ranunculaceae		FM242782	FM242846	FM242846	FM242846		
RUMEX ACETOSELLA	Polygonaceae	D86290	EF438022	AF189730	AF189730	AF189730		
SANICULA BIPINNATIFIDA	Apiaceae			EU070745	EU070745	EU070745		
SANICULA ELATA	Apiaceae	AM234825		AF031966	AF031966	AF031966		yes
SILENE GALLICA	Caryophyllaceae	M83544	FJ589528	U30959	U30985	U30985		
SILYBUM MARIANUM	Asteraceae		X81106	EU592013	EU592013	AF319148		
SISYRINCHIUM BELLUM	Iridaceae	AY149369					Sisyrinchium montanum	
TAENIATHERUM CAPUT-MEDUSAE	Poaceae	AY836184		EU883118	AJ608153	AJ608153		

THYSANOCARPUS CURVIPES	Brassicaceae			EU620333	EU620333	EU620333	
THYSANOCARPUS LACINIATUS	Brassicaceae			GU246179	GU246179	GU246179	
TIGRIDIA ALPESTRIS	Iridaceae	AM940191	AM940214				yes
TORILIS ARVENSIS	Apiaceae	AM234827		AF164843		AF164869	
TORILIS JAPONICA	Apiaceae	FJ395562		EU236214	EU236214	EU236214	yes
TORILIS NODOSA	Apiaceae			U30534		U30535	
TRIFOLIUM ALBOPURPUREUM	Fabaceae		AF522116	AF053143	AF053143	AF053143	
TRIFOLIUM BIFIDUM	Fabaceae			AF053156	AF053156	AF053156	
TRIFOLIUM CILIOLATUM	Fabaceae			AF053152	AF053152	AF053152	
TRIFOLIUM DEPAUPERATUM	Fabaceae			AF004305	AF004305	AF004305	
TRIFOLIUM DUBIUM	Fabaceae		AF522121	DQ312047	DQ312047	DQ312047	
TRIFOLIUM GRACILENTUM	Fabaceae		AF522123	DQ312060	DQ312060	DQ312060	
TRIFOLIUM HIRTUM	Fabaceae		AF522124	AF154359	AF053158	AF053158	
TRIFOLIUM MICROCEPHALUM	Fabaceae		AF522128	DQ312092	DQ312092	DQ312092	
TRIFOLIUM MICRODON	Fabaceae			DQ312093	DQ312093	DQ312093	

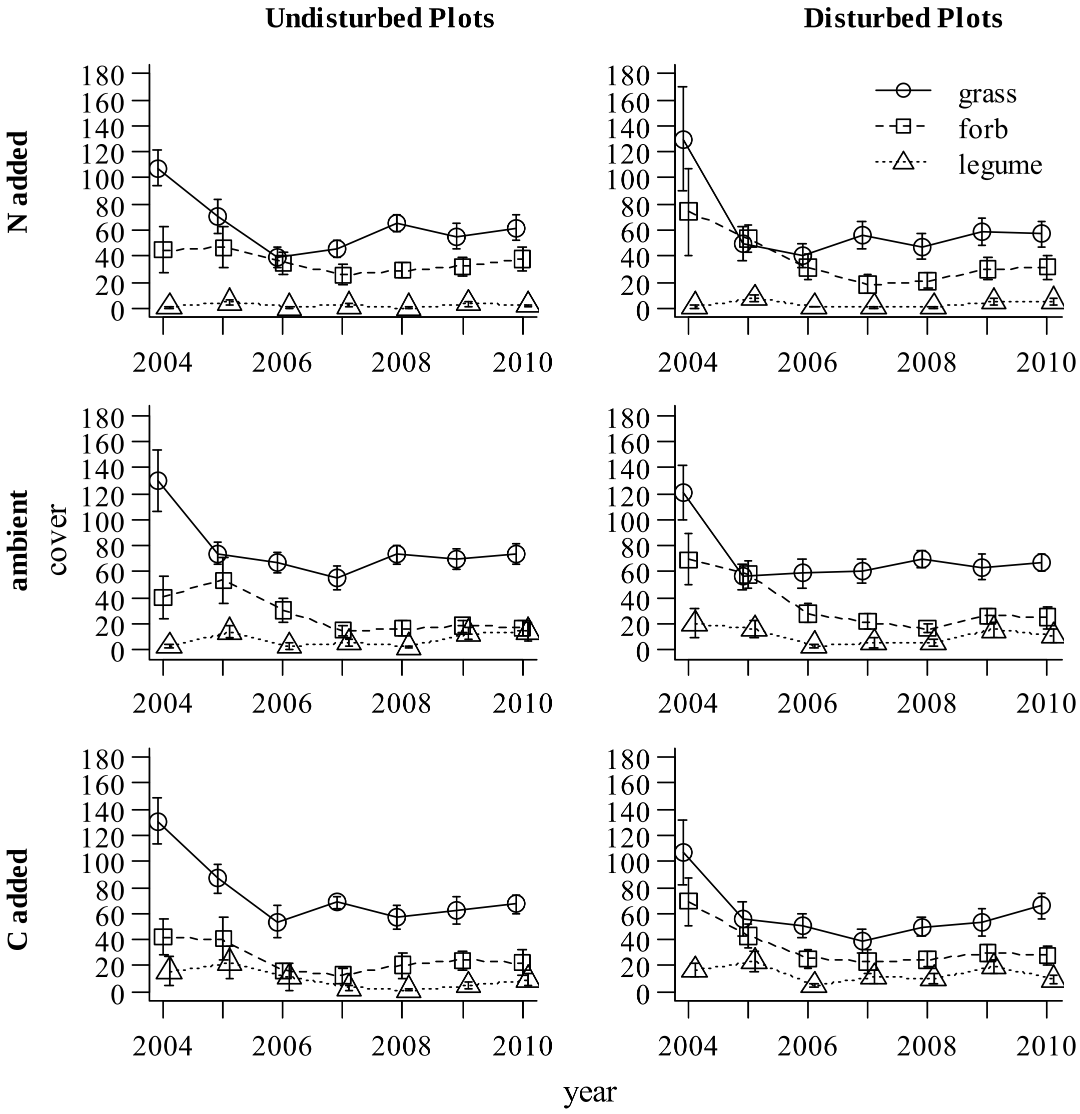
TRIFOLIUM OBTUSIFLORUM	Fabaceae			DQ312106	DQ312106	DQ312106		
TRIFOLIUM SPECIES1	Fabaceae							
TRIFOLIUM SPECIES2	Fabaceae							
TRIFOLIUM WILLDENOVII	Fabaceae		AF522137	DQ312194	DQ312194	DQ312194		
TRIPHYSARIA ERIANTHA	Orobanchaceae			EF103735	EF103735	EF103735		
TRITELEIA LAXA	Themidaceae	AJ311070					Triteleia peduncularis	
UROPAPPUS LINDLEYI	Asteraceae		AJ633242	AJ581703	AJ581703	AJ581703		
VICIA SPECIES	Fabaceae		AF522161	DQ312199	DQ312199	DQ312199	Vicia villosa	
VIOLA DOUGLASII	Violaceae			AF097229		AF097275	Viola purpurea	
VIOLA PEDUNCULATA	Violaceae			AF097227		AF097273	Viola beckwithii	
VIOLA VERECUNDA	Violaceae	DQ834758	DQ842581	AY928283	AY928283	AY928283		yes
VULPIA BROMOIDES	Poaceae		FJ395408	AF478485	AF478485	AF478485		
VULPIA MICROSTACHYS	Poaceae		DQ786948	EF584981	EF584981	EF584981		
VULPIA MYUROS	Poaceae		AF164403	AJ240162	AJ240162	AJ240162		
ZELTNERA TRICHANTHA	Gentianaceae			AY047710		AY047795		yes

Appendix J



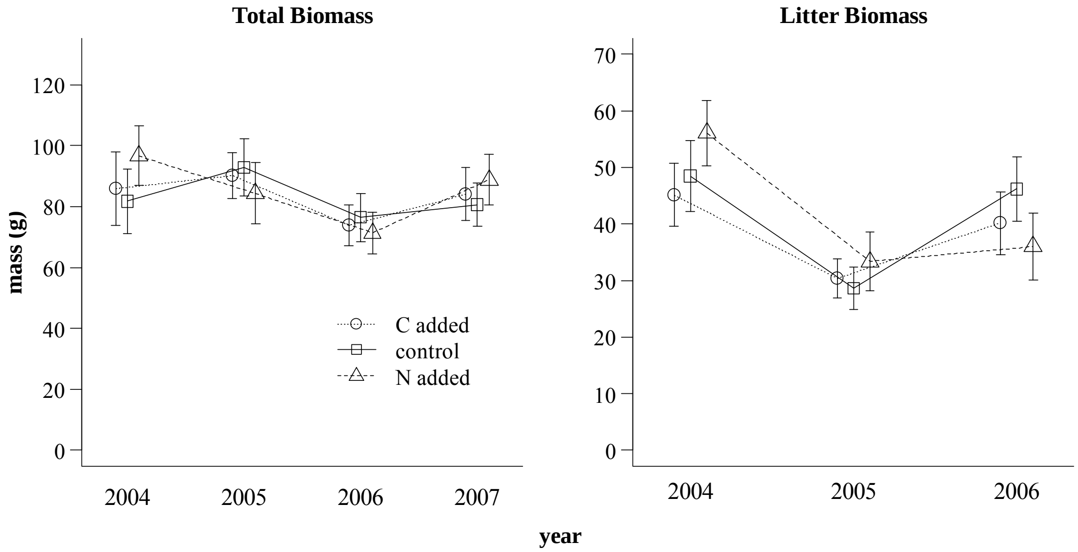
Appendix J: Maximum likelihood phylogeny of all species listed in Appendix I with nodal support values.

Appendix K



Appendix K: Cover of functional groups (grass, non-leguminous forb, and leguminous forb) in grassland plots from 2004-2010 receiving a factorial combination of disturbance and nitrogen supply treatments. Undisturbed plots are in the left column; disturbed plots in the right. Nitrogen addition represented an augmentation (top row), control plots were unmanipulated (middle row), and carbon addition represented nitrogen reduction (bottom row).

Appendix L



Appendix L: Total aboveground biomass (left) and litter biomass (right) collected in grassland plots receiving three levels of nitrogen manipulation: reduction (carbon addition), ambient levels (control), and augmentation (nitrogen addition).

Appendix M

Appendix M: Biomass (means and SD, n=8) of the six focal grass species in experimentally-established field communities at Sedgwick Reserve from 2001 to 2005. Focal species are three native perennial and three exotic annual grasses from three tribes. Plot treatments were: 1) established native perennial grass-dominated, 2) exotic annual grass-dominated, and 3) cross-seeded native perennial and exotic annual grass.

Species	Tribe	Life History (Provenance)	Year	Biomass (g)		
				Native Perennial Plots	Exotic Annual Plots	Cross-seeded Plots
Bromus carinatus	Bromeae	Perennial (native)	2001	28.92 ± 20.54	8.74 ± 12.60	77.33 ± 63.65
			2002	22.06 ± 43.71	14.43 ± 19.84	8.51 ± 9.50
			2003	4.37 ± 5.07	21.49 ± 43.28	15.49 ± 36.15
			2004	3.37 ± 6.35	4.07 ± 9.77	1.03 ± 1.70
			2005	6.31 ± 17.85	19.26 ± 53.30	1.77 ± 3.01
Bromus hordeaceus	Bromeae	Annual (exotic)	2001	42.16 ± 33.60	78.5 ± 100.82	59.68 ± 69.49
			2002	29.87 ± 34.86	61.38 ± 46.43	35.08 ± 25.22
			2003	87.84 ± 79.08	99.49 ± 55.03	90.09 ± 37.40
			2004	33.06 ± 27.95	89.79 ± 67.50	43.44 ± 25.86
			2005	110.52 ± 89.57	132.66 ± 72.54	126.48 ± 111.90
Bromus madritensis	Bromeae	Annual (exotic)	2001	2.29 ± 3.32	79.51 ± 82.82	61.35 ± 74.56
			2002	0.12 ± 0.23	19.51 ± 32.68	9.37 ± 16.11
			2003	5.31 ± 9.63	21.15 ± 21.41	12.76 ± 12.74
			2004	0.73 ± 1.37	5.73 ± 7.50	1.92 ± 2.92
			2005	0.88 ± 1.48	3.44 ±	4.21 ±

					6.08	7.75
Elymus glaucus	Triticeae	Perennial (native)	2001	25.55 ± 35.83	2.04 ± 4.70	5.96 ± 12.77
			2002	14.42 ± 33.31	3.28 ± 5.81	21.36 ± 37.57
			2003	26.60 ± 32.09	29.02 ± 27.15	61.82 ± 48.86
			2004	7.18 ± 12.50	20.13 ± 35.87	15.16 ± 21.72
			2005	21.11 ± 45.49	56.42 ± 61.17	143.25 ± 143.92
Hordeum murinum	Triticeae	Annual (exotic)	2001	0.08 ± 0.23	7.64 ± 9.93	11.26 ± 12.57
			2002	0.00 ± 0.00	3.45 ± 8.92	1.54 ± 2.59
			2003	0.00 ± 0.00	11.00 ± 21.16	1.68 ± 2.58
			2004	0.00 ± 0.00	0.60 ± 0.69	0.95 ± 1.30
			2005	0.00 ± 0.00	2.33 ± 3.92	0.25 ± 0.28
Nassella pulchra	Stipeae	Perennial (native)	2001	99.94 ± 35.73	1.15 ± 1.11	8.59 ± 10.55
			2002	62.16 ± 47.41	1.23 ± 1.46	8.45 ± 7.50
			2003	82.71 ± 73.91	1.66 ± 3.14	11.51 ± 11.54
			2004	61.81 ± 48.06	3.87 ± 8.71	1.10 ± 1.36
			2005	78.90 ± 59.24	11.76 ± 33.25	24.91 ± 66.38

Appendix N

Appendix N: Responses (means and SD) of the six focal grass species grown in pots containing whole-soil inoculum collected from experimental field plots ("Inoc") vs. sterilized soil ("Sterile"). Focal species are three native perennial and three exotic annual grasses from three tribes.

Species	Tribe	Life History (Provenance)	*n*		Biomass (g)		Root-shoot ratio		Time to half max height (days)		Max Growth Rate (mm/day)	
			Inoc	Sterile	Inoc	Sterile	Inoc	Sterile	Inoc	Sterile	Inoc	Sterile
Bromus carinatus	Bromeae	Perennial (native)	24	8	1.40 ± 0.38	2.06 ± 0.47	1.06 ± 0.30	1.29 ± 0.29	25.56 ± 8.72	25.82 ± 7.21	0.07 ± 0.02	0.06 ± 0.02
Bromus hordeaceus	Bromeae	Annual (exotic)	24	8	1.31 ± 0.16	1.36 ± 0.34	0.99 ± 0.18	0.88 ± 0.29	32.18 ± 3.59	29.00 ± 4.21	0.08 ± 0.02	0.07 ± 0.02
Bromus madritensis	Bromeae	Annual (exotic)	23	8	1.44 ± 0.22	1.55 ± 0.34	0.52 ± 0.34	0.70 ± 0.38	25.06 ± 12.15	29.56 ± 3.34	0.08 ± 0.02	0.08 ± 0.02
Elymus glaucus	Triticeae	Perennial (native)	24	8	1.22 ± 0.33	1.32 ± 0.39	1.08 ± 0.35	1.03 ± 0.19	17.50 ± 15.90	12.50 ± 15.54	0.06 ± 0.02	0.06 ± 0.02
Hordeum murinum	Triticeae	Annual (exotic)	22	7	1.13 ± 0.30	1.83 ± 0.39	0.77 ± 0.19	0.97 ± 0.27	27.29 ± 12.54	17.47 ± 10.17	0.10 ± 0.02	0.09 ± 0.02
Nassella pulchra	Stipeae	Perennial (native)	24	8	0.61 ± 0.21	0.56 ± 0.43	0.43 ± 0.12	0.46 ± 0.20	14.15 ± 45.59	37.46 ± 21.22	0.04 ± 0.02	0.05 ± 0.01

Appendix O

Appendix O: Responses (means and SD) of the six focal grass species grown in pots containing whole-soil inoculum collected from natural grassland communities. Focal species are three native perennial and three exotic annual grasses from three tribes.

Species	Tribe	Life History (Provenance)	Biomass (g)	Root-shoot ratio	Time to half max height (days)	Max Growth Rate (mm/day)
Bromus carinatus	Bromeae	Perennial (native)	1.19 ± 0.24 (*n* = 7)	0.91 ± 0.21 (*n* = 7)	19.74 ± 29.01 (*n* = 7)	0.06 ± 0.02 (*n* = 7)
Bromus hordeaceus	Bromeae	Annual (exotic)	1.08 ± 0.27 (*n* = 8)	0.84 ± 0.19 (*n* = 8)	25.52 ± 8.53 (*n* = 8)	0.07 ± 0.02 (*n* = 8)
Bromus madritensis	Bromeae	Annual (exotic)	1.20 ± 0.25 (*n* = 8)	0.56 ± 0.23 (*n* = 8)	24.92 ± 8.30 (*n* = 8)	0.06 ± 0.01 (*n* = 8)
Elymus glaucus	Triticeae	Perennial (native)	1.17 ± 0.25 (*n* = 8)	1.10 ± 0.22 (*n* = 8)	4.75 ± 25.55 (*n* = 8)	0.05 ± 0.01 (*n* = 8)
Hordeum murinum	Triticeae	Annual (exotic)	1.12 ± 0.26 (*n* = 8)	0.83 ± 0.25 (*n* = 8)	23.83 ± 6.39 (*n* = 7)	0.10 ± 0.02 (*n* = 7)
Nassella pulchra	Stipeae	Perennial (native)	0.52 ± 0.13 (*n* = 8)	0.43 ± 0.17 (*n* = 8)	2.40 ± 56.61 (*n* = 8)	0.04 ± 0.01 (*n* = 8)