1-1-2005

Plant species turnover as a mechanism of community change in response to biotic and abiotic perturbation

Kathryn Anne Yurkonis
Eastern Illinois University

Recommended Citation

Yurkonis, Kathryn Anne, "Plant species turnover as a mechanism of community change in response to biotic and abiotic perturbation" (2005). *Masters Theses*. 929.
http://thekeep.eiu.edu/theses/929

THESIS REPRODUCTION CERTIFICATE

TO: Graduate Degree Candidates (who have written formal theses)

SUBJECT: Permission to Reproduce Theses

The University Library is receiving a number of request from other institutions asking permission to reproduce dissertations for inclusion in their library holdings. Although no copyright laws are involved, we feel that professional courtesy demands that permission be obtained from the author before we allow these to be copied.

PLEASE SIGN ONE OF THE FOLLOWING STATEMENTS:

Booth Library of Eastern Illinois University has my permission to lend my thesis to a reputable college or university for the purpose of copying it for inclusion in that institution's library or research holdings.

______________________	6/16/05
Author's Signature	Date

I respectfully request Booth Library of Eastern Illinois University **NOT** allow my thesis to be reproduced because:

____

____

____

______________________	______________
Author's Signature	Date

This form must be submitted in duplicate.

PLANT SPECIES TURNOVER AS A MECHANISM OF COMMUNITY CHANGE IN RESPONSE TO BIOTIC AND ABIOTIC PERTURBATION

BY

KATHRYN ANNE YURKONIS

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE - BIOLOGICAL SCIENCES

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2005

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED AS FULFILLING
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

6/16/2005
DATE

THESIS DIRECTOR

June 16, 2005
DATE

DEPARTMENT/SCHOOL HEAD

ABSTRACT

Plant communities change through time as species respond to changes in their biotic and abiotic environment. Biotic factors influencing plant communities can include species invasion, competition, or herbivory, whereas abiotic factors can include drought, fire, or nutrient deposition. Although factors influencing community structure have been extensively documented, the mechanisms by which communities respond to disturbances are not well understood. To address this problem, my thesis research considered two perturbations, exotic species invasion and drought, in each case I specifically relate species turnover to changes in community structure. The overall goal of this project was to evaluate the utility of using species turnover dynamics as a simple conceptual framework for assessing general mechanisms of community change. I determined species turnover at the community and population scales to identify 1) the mechanisms driving exotic species impacts and 2) the mechanisms of community change associated with drought.

Exotic species invasion resulted in declines in diversity caused by reduced colonization rates, and not increased extinction rates for all invaders. Populations differed in their susceptibility to invasion impacts, with most species showing reduced colonization rates. These results suggest that establishment limitation may be a general mechanism of invasion impacts. During a two-month drought, diversity and cover declined due to both reduced colonization and increased extinction rates. Diversity and cover quickly rebounded in this system during a colonization window opened by drought. Surprisingly, drought had little long-term effect on community structure and initiated only subtle changes in the understory community composition. Population dynamics appeared to be generally driven by stochastic species turnover within sites and not by large-scale shifts in species performance.

Within this system, community response to perturbation appears to be primarily driven by colonization dynamics. In both perturbation scenarios, exotic species invasion and drought, colonization rates changed and led to altered community composition. Although the mechanisms of community change were uniform across disturbance type, changes occurred at a local scale and not uniformly across the entire community. The study resulted in several interesting findings that improved our understanding of the mechanisms governing community response to disturbance and allowed us to make testable predictions on the response of communities to disturbance. This approach can be used in other systems to determine the generality of these mechanisms as drivers of community change across a suite of disturbance types.

ACKNOWLEDGEMENTS

I owe much credit for my success in the past two years to my advisor Scott J. Meiners who spent countless hours brainstorming and discussing ideas concerning this and other projects. His encouragement and devotion to his students were crucial in developing this project and helping me grow as a scientist. I could not have asked for a better Master's advisor. By the way the new office looks great and thanks for the raise. I also thank my committee members Eric K. Bollinger and Robert U. Fischer for teaching me a thing or two in the past two years.

My labmates Matt Burmiester, Jamie Jordan, Lydia Miramontes, William Stewart, Elise Tulloss, and Brent Wachholder helped immensely by reviewing proposals and manuscripts. Heather MacFarland was influential in organizing the first stages of the exotic species project and several anonymous reviewers provided constructive criticism on the exotic species chapter. Finally, this project would not have been possible without all those that have sampled plots and entered data for the Buell-Small Succession Study.

The crazy people that dissect turkey eggs and dead deer for the fun of it (my family and friends) were helpful in keeping a smile on my face. Thanks for encouraging me to tromp around in the woods.

This research was supported by NSF grant DEB-0424605, USDA CSREES grant 99-35315-7695, and separate grants from the Council on Faculty Research and Graduate School of Eastern Illinois University.

TABLE OF CONTENTS

TABLES

TABLE **PAGE**

CHAPTER 1

CHAPTER 2

FIGURES

FIGURE PAGE

CHAPTER 1

CHAPTER 2

INTRODUCTION

Plant communities change through time as species respond to changes in their biotic and abiotic environments. Biotic factors influencing plant communities can include species invasion, competition or herbivory, whereas abiotic factors can include drought, fire or nutrient deposition. Although factors influencing community structure have been extensively documented, the mechanisms by which communities and their populations respond to disturbances are not well understood. Only with an understanding of the mechanisms driving community response and recovery from disturbance can we begin to predict and manage community responses to disturbance.

One way to assess how communities change with disturbance is to quantify species turnover within the system. Local species richness or abundance is a function of the local colonization and extinction rates (MacArthur & Wilson 1967; Levins 1969). Thus, changes in local diversity with perturbation result from changes in the balance between local colonization and extinction rates. Each suggests different mechanisms of community change. If colonization rates change with disturbance then establishment limitation is involved in community response to disturbance. If extinction rates change then competition or other sources of mortality are structuring the community. In some instances both colonization and extinction rates may change in association with a disturbance to influence future community structure and composition. This conceptual framework can be applied to any dynamic system to assess mechanisms behind community change.

Species turnover can be quantified at both the population and the community scale. As net community impacts inherently result from population responses (Pickett &

Cadenasso 2005), species turnover dynamics can be used as a tool to relate community and population responses to disturbance. By assessing disturbance impacts within the framework of species turnover dynamics we can determine the relationships between species interactions, community dynamics, and the overall changes seen in the community.

My thesis research considered two disturbance scenarios, exotic species invasion and drought, in a successional system. I determined rates of species turnover at the community and population scales to broadly identify 1) the mechanisms driving exotic species impacts and 2) the mechanisms of community change associated with drought. Answers to these questions can be used to predict and manage community response to disturbance in successional systems.

Study System

I used data collected from abandoned agricultural land in New Jersey, as part of the Buell-Small Succession Study (BSS), initiated in 1958 and most recently sampled in 2004. The study site consists of 10 fields each containing 48 permanently marked 1 m^2 plots that are sampled yearly for percent cover of all species. The extensive nature of this dataset allows for detailed analysis of vegetation change over time, a rare opportunity in the study of plant communities. I specifically documented species turnover dynamics at the community and population scales to investigate the mechanisms of community change in response to exotic species invasion and drought.

Mechanisms of exotic species impacts

I used the BSS data to examine turnover dynamics to determine the mechanism(s) of invasion impacts of four exotic species of different lifeforms (grass, biennial, liana and shrub). Community diversity, colonization and extinction rates were compared to invasion intensity using statistical models.

Mechanisms of community response to drought

I also used BSS data to examine community response to and recovery from drought. Trends in community diversity, cover, colonization and extinction rates were analyzed over a period of seven years (1997 to 2003) spanning a severe drought (1999) in separate statistical analyses. At the population scale, cover trends of six drought susceptible species were also analyzed over the seven-year period. To assess changes in community composition plot species richness, species occurrences and species cover were compared before and after drought.

Mechanisms of community change

The overall goal of this project is to evaluate the utility of using species turnover dynamics as a simple conceptual framework for assessing mechanisms of community change. If successful, this conceptual framework can be applied in other systems to identify if generalities exist in the mechanisms governing community structure and composition.

CHAPTER 1

INVASION IMPACTS ON COMMUNITY DYNAMICS

Abstract

Invading plant species often alter community structure, composition and, in some instances, reduce local diversity. However, the community dynamics underlying these impacts are relatively unknown. Declines in species richness with invasion may occur via displacement of resident species and/or reduction of seedling establishment by the invader. These two mechanisms differ in the demographic stage of the interaction. I document turnover dynamics using long-term permanent plot data to assess the mechanism(s) of invasion impacts of four exotic species on a mixed community of native and exotic species. These mechanisms were evaluated at both the neighborhood ($1m^2$ plot) and population (individual species) scales. During invasion, species richness declined with increasing invader cover for three of the four invaders. All invaders reduced colonization rates, but had no effect on extinction rates at the neighborhood scale. Populations differed in their susceptibility to invasion impacts, with significant reductions in colonization for 10 of 25 (40%) species and increases in extinction for only 4 of 29 (14%) species. At neighborhood and population scales, influences of invasion on community dynamics were essentially the same for all invaders regardless of lifeform. While individual resident species had some increase in extinction probability, community richness impacts were largely driven by colonization limitation. The consistency of invasion impacts across lifeforms suggests establishment limitation as a general mechanism of invasion impact. This common causal mechanism should be explored in other systems to determine the extent of its generality.

Introduction

Exotic species invasion is a biological disturbance affecting ecosystems worldwide, and in some cases invasion can have large effects. Invading species can affect the trajectory of invaded vegetation by altering natural disturbance regimes (Mack & D'Antonio 1998) and reducing diversity (Meiners *et al.* 2001). In addition, invasion can affect plant communities by altering resource dynamics (Vitousek *et al.* 1987; Ehrenfeld 2003) and interspecific interactions (D'Antonio *et al.* 1998; Christian & Wilson 1999). However, not all species have these impacts; only a select few cause large changes within invaded communities (Williamson 1996; Levine *et al.* 2003). Despite the magnitude of invasions occurring across the world, the mechanisms underlying invasion impacts are not well understood (Blossey 1999; Parker *et al.* 1999; Byers *et al.* 2002; Levine *et al.* 2003).

Invasive species are often noted for their tendency to alter species richness within invaded communities (Rejmánek & Rosén 1992; Hager & McCoy 1998; Parker *et al.* 1999; Meiners *et al.* 2001). Proposed mechanisms explaining invader effects on community diversity can be divided according to the demographic stage which is impacted by the invasion. The invader can either affect resident species established within the community (species displacement), inhibit the establishment of new individuals (establishment limitation), or both.

Resident species displacement, where plant invaders reduce local diversity by displacing established species, has been the most widely suggested mechanism of invasion impacts (Hager & McCoy 1998; Parker *et al.* 1999, reviewed in Levine *et al.* 2003). Such displacement may occur through resource competition where the invader more readily secures limiting resources (Schoener 1983; Tilman 1997), exhibits allelopathic effects that suppress neighboring species (Callaway & Aschehoug 2000), or develops antagonistic soil microbial feedbacks (Bever 2003; Callaway *et al.* in press).

Invasion can also affect the community via establishment limitation by reducing colonization success of resident species (Crawley *et al.* 1999; Cahill 2003; Seabloom *et al.* 2003, Hager 2004; Yurkonis & Meiners 2004). This may result from site saturation by invader propagules (Brown & Fridley 2003), which take up available germination sites, reducing establishment rates of other species. Similarly, reductions in resource availability have also been shown to reduce local establishment. Communities with relatively low levels of available resources are often resistant to the establishment of new colonists (Tilman 1993; Burke & Grime 1996; Knops *et al.* 1999; Davis *et al.* 2000; Symstad 2000; Cahill 2003, Cleland *et al.* 2004). However, increased resource availability has also been shown to decrease colonization rates (Stevens *et al.* 2004) through increasing stem density. Where competitive interactions shape community structure, invasion may more strongly inhibit colonization of species within the same functional group as the invader (Prieur-Richard *et al.* 2000; Symstad 2000; Fargione *et al.* 2003) due to more similar resource requirements. These potential effects of invasion may become magnified in systems already limited via dispersal of native seed (Seabloom *et al.* 2003), in highly fertile sites (Cleland *et al.* 2004; Stevens *et al.* 2004) or those recovering from disturbance events (Stampfli & Zeiter 2004) where re-colonization is limited.

Collectively, invasion impacts on communities, through any mechanism, have been documented with few species and mostly anecdotal evidence (Parker *et al.* 1999; Levine *et al.* 2003). In order to properly assess invasion impacts, local turnover dynamics in relation to changes in species richness must be examined within a system. Within communities, species richness is a balance between colonization and extinction rates (MacArthur & Wilson 1967). Therefore, if an invading species causes a change in local species richness, this change must reflect a change in the balance between local colonization and extinction rates, and the turnover rates of individual species (Levins 1969; Ouborg 1993; Husband & Barrett 1996; Blomqvist *et al.* 2003).

By identifying how community dynamics change with invasion, I can then isolate the demographic stage of the interactions driving invasion impacts. Increased extinction rates reflect invasion interactions with resident species and indicate that species displacement mechanisms drive invasion impacts. Decreased colonization rates reflect limitations on local establishment and indicate that invader-seedling interactions drive invasion impacts. Overall, the impact of invasion on community dynamics reflects net displacement and establishment limitation effects. Therefore even simple community associations may result from more complex underlying species interactions.

In this study I examined species turnover dynamics associated with four exotic species invasions to explicitly determine the mechanism(s) of invasion impacts on species richness. I calculated turnover dynamics based upon 46 years of vegetation data from a series of abandoned agricultural fields in the New Jersey Piedmont region. I used these data to determine: 1) Does invasion relate to changes in community species richness, and, if so, 2) Does invasion primarily change colonization and/or extinction rates, and 3) Do similar trends occur at the neighborhood and population scales in the impact of invasion?

Methods

Study System

I used data collected on the invasion of four exotic species into abandoned agricultural land in the Piedmont region of New Jersey, USA (40°30' N, 74°34' W) as part of the Buell-Small Succession Study (BSS). Initiated in 1958, the study consists of 10 agricultural fields abandoned in pairs over a period of 8 years (Buell *et al.* 1971; Pickett 1982). Fields differed in season of abandonment, last crop and final plowing regime to assess the impact of different disturbance legacies on succession (Myster & Pickett 1990). Within each field, 48 permanently-marked 0.5 × 2.0 m plots were established immediately after abandonment (Pickett 1982). In each year (alternate years since 1979), the percent cover of all species present in each plot was recorded. As plants often have overlapping canopies, total plant cover may greatly exceed 100% within each plot. These data represent the longest continuous data set on post-agricultural successional change known. Nomenclature follows Gleason & Cronquist (1991).

The successional dynamics of this system are well characterized. Of the 342 species identified within the study, 222 (65%) are native. Despite the variation in pre-abandonment conditions, the general successional trajectories of all fields are remarkably similar, though composition often varied dramatically as did the rate of successional change (Myster & Pickett 1990; 1994). While the fields accumulated species over successional time, the number of species in each $1 m^2$ plot remained constant at about 13 species (Meiners *et al.* 2002). Interestingly, the total number of exotic species found in the fields also decreased over time. Because the majority of exotic species within the site are ruderals characteristic of agricultural systems, the abundance of exotic species was initially high (>50% relative cover) but has declined through succession to approximately 30% relative cover (Meiners *et al.* 2002).

A preliminary study of 14 native and 12 exotic taxa that became abundant during succession found only five species whose invasions were associated with declines in species richness (Meiners *et al.* 2001). These species included four exotics of Eurasian origin: *Elytrigia repens* (L.) Nevski. (perennial grass), *Lonicera japonica* Thunb. (liana), *Rosa multiflora* Thunb. (shrub), and *Trifolium pratense* L. (leguminous short-lived perennial herb), with only a single native species, *Solidago canadensis* L. (perennial herb). More detailed analyses, however, found no influence of *S. canadensis* on species richness, community colonization/extinction dynamics, or any individual resident species (Yurkonis unpublished data). The current study, therefore, specifically focused on the four exotic invaders to determine the mechanism(s) that generated their community-level impacts.

Data Analyses

To evaluate community dynamics in response to invasion, I determined changes in plot composition between the time of the initial invasion ($T_{initial}$) and peak of invader cover (T_{peak}) based on average coverage and frequency across all invaded fields (Fig. 1). I then used change in invader cover ($T_{peak} - T_{initial}$) as a measure of invasion magnitude in each plot (Meiners *et al.* 2001; Yurkonis & Meiners 2004). The time of initial invasion represents when low frequency and cover of the invader was observed across the site, rather than, necessarily, the time of initial invasion within individual plots. Because fields varied in abandonment over an 8 calendar-year period, time was measured as years since abandonment. Study periods ($T_{initial}$ to T_{peak}) for each invader are as follows: *Elytrigia repens* 1 to 5 years since abandonment, *Lonicera japonica* 5 to 15 years since abandonment, *Rosa multiflora* 10 to 20 years since abandonment and *Trifolium pratense* 1 to 4 years since abandonment (Fig. 1).

While this results in differing sample periods for each invader, the resulting time periods closely match the lifespan and turnover of the resident species dominant during each invasion (Von Holle *et al.* 2003). Early invaders *E. repens* and *T. pratense* invaded systems dominated by short-lived species with relatively rapid turnover (5 years or less), while the later invaders *R. multiflora* and *L. japonica* invaded systems dominated by longer lived species with slower turnover (>10 years). *Elytrigia repens* and *T. pratense* invaded four of the 10 fields while *L. japonica* and *R. multiflora* invaded all fields across the site. Because diversity is often associated with plot invasibility in this system (Meiners *et al.* 2004), analyses were limited to invaded plots for each species.

Analyses were conducted at two ecological scales, neighborhood and population, to determine the mechanism(s) that generate invasion impacts within these successional fields. The neighborhood scale, hereafter defined as the local community within each plot, is the scale at which species interact to generate invasion impacts. The neighborhood scale was used to assess impacts of invaders on species richness, colonization rates and extinction rates. To determine the mechanism(s) responsible for neighborhood level dynamics, population scale analyses were conducted. At the population scale, I examined species-species interactions to determine the influence of invasion on the colonization and extinction dynamics of individual resident species based on plot occupancy.

Neighborhood Dynamics

To document impacts of each invader on neighborhood dynamics, I related the change in species richness ($S_{peak} - S_{initial}$) to the magnitude of invasion for each plot (Meiners *et al.* 2001; Yurkonis & Meiners 2004). The relationship between magnitude of invasion and change in species richness was analyzed with ANCOVA using field identity as a categorical variable and invasion magnitude as a continuous one. Neighborhood colonization and extinction rates were calculated for each plot as the number of new species gained or lost between $T_{initial}$ and T_{peak}. Although multiple colonization and extinction events may have occurred over invasion study periods, our measures of colonization and extinction reflect net changes in composition. The utility of this approach is that it would tend to only include successful colonizations (or extinctions) rather than including minor fluctuations. As before, ANCOVA was used to simultaneously evaluate field and invader impacts on dynamics. Analyses of the residuals for all comparisons did not indicate the need for any data transformations.

Population Dynamics

Colonization and extinction rates were also determined for individual species, regardless of nativity, in association with each invader. Since successional systems are typically heavily invaded by exotic species (Bard 1952; Inouye *et al.* 1987; Rejmánek 1989; Bazzaz 1996), many of the residents examined are themselves naturalized exotics. This holistic approach generates a more realistic view of invader impacts than focusing solely on natives and ignoring Eurasian species that have become common constituents of the community.

All species that colonized or went extinct in 100 or more of the 480 ($\geq$ 21%) plots during each invasion were selected for analysis. Species selection was based upon the natural break in frequency of plot colonization and extinction. Species below this break tended to invade or go extinct in relatively few plots. Less-frequent species, although potentially important in neighborhood response to invasion, were not assessed within this study because of the weak statistical power associated with lower frequencies. Colonization/extinction rates were then determined individually for each species that met this criterion.

Colonization and extinction rates were calculated for each plot as the number of new species gained or lost between $T_{initial}$ and T_{peak} for each of the invaders. Although multiple colonization and extinction events may have occurred over the invasion period, our measures of colonization and extinction reflect net changes in community composition because I examined the endpoints only. The utility of this approach is that it would tend to only include successful colonizations (or extinctions) rather than including all unsuccessful events. Logistic regressions were used to relate probability of colonization/extinction for each species to invasion intensity in each plot. A Dunn-Sidák correction for multiple comparisons was used to adjust the significance criterion and results are reported at the $P = 0.10$ and $P = 0.05$ level. As these population patterns are used to explain dynamics at the neighborhood scale, the lower significance criterion are included to identify potential interactions that generate net invasion impacts.

Results

Neighborhood responses to invasion

Neighborhood species richness declined with invasion intensity for three of the four invaders (Fig. 2). *Trifolium pratense* ($F_{1,120} = 6.29$; $P = 0.013$, $R^2 = 0.471$), *Lonicera japonica* ($F_{1,207} = 4.12$; $P = 0.044$, $R^2 = 0.433$) and *Rosa multiflora* ($F_{1,180} = 6.91$; $P = 0.009$, $R^2 = 0.201$) all showed significant associations with declines in neighborhood species richness during their invasions. There were no interactions between invasion intensity and field for any of the invaders. However, field was a significant determinant of change in neighborhood richness during the *E. repens* ($F_{3,79} = 5.31$; $P = 0.002$, $R^2 = 0.684$) and *L. japonica* ($F_{9,207} = 6.67$; $P < 0.001$) invasions. The invasion of *E. repens* was not related to changes in species richness.

Neighborhood colonization rates declined with increased invasion intensity for all species (Fig. 3; *Trifolium pratense* - $F_{1,120} = 4.15$; $P = 0.044$, $R^2 = 0.377$; *Elytrigia repens* – $F_{1,79} = 15.01$; $P < 0.001$, $R^2 = 0.739$; *Lonicera japonica* – $F_{1,207} = 5.96$; $P = 0.015$, $R^2 = 0.319$; *Rosa multiflora* – $F_{1,180} = 10.76$; $P = 0.001$, $R^2 = 0.154$). Field was a significant determinant of colonization rate in association with *E. repens* ($F_{3,79} = 29.51$; $P < 0.001$) and *L. japonica* ($F_{9,207} = 3.59$; $P < 0.001$) invasions though there were no interactions between invasion intensity and field for any of the exotic species. In contrast, neighbourhood extinction rates were not affected by any of the invasions (Fig. 4) and were solely determined by field (*Trifolium pratense* – $F_{3,120} = 2.81$; $P = 0.042$, $R^2 = 0.428$; *Elytrigia repens* – $F_{3,79} = 26.62$; $P < 0.001$, $R^2 = 0.770$; *Lonicera japonica* – $F_{9,207} = 2.94$; $P = 0.003$, $R^2 = 0.234$; *Rosa multiflora* – $F_{9,180} = 2.51$; $P = 0.010$, $R^2 = 0.271$).

Population responses to invasion

Invasion was associated with declines in colonization rates for 10 of 25 (40%) common species (Table 1), following the neighborhood level pattern. Invasions of *Lonicera japonica*, *Rosa multiflora* and *Trifolium pratense* were also associated with increased extinction rates for 4 of 29 (14%) species (Table 2). *Elytrigia repens* showed no effects on population extinction rates. All impacts, regardless, of significance level, were negative and I found no facilitative interactions with invasion. Species affected by invasion either through decreased colonization rates or increased extinction rates primarily consisted of a variety of wind-dispersed perennials. Multiple invaders were found to influence turnover dynamics of individual resident species.

Table 1 Results of logistic regression of colonization rates of common species with invasion intensity for four exotic species. Of all the species assessed, only species with significant associations are shown. Colonization rates and invasion intensity were assessed on a plot-by-plot basis for the invasion window selected for each species. Each term is associated with 1 df. Nativity and lifeforms are indicated in parentheses following each species: N=native, E=exotic, A = annual, B = biennial/short-lived perennial, G = grass, L = liana, P = perennial, S = shrub, T = tree.

Invader	Species	β	Wald χ^2
Trifolium pratense[1]	*Aster pilosus* (NB)	-0.026	7.893*
	Hieracium caespitosum (EP)	-0.038	8.396*
	Rumex acetosella (EP)	-0.021	6.756†
Elytrigia repens[2]	*Aster pilosus* (NB)	-0.029	8.774*
	Daucus carota (EB)	-0.027	7.251*
Lonicera japonica[3]	*Achillea millefolium* (NP)	-0.017	9.248*
	Oxalis stricta (NP)	-0.021	9.261*
	Solidago rugosa (NP)	-0.017	8.661*
Rosa multiflora[4]	*Juniperus virginiana* (NT)	-0.017	7.583†
	Poa compressa (EG)	-0.013	7.452†
	Solidago juncea (NP)	-0.017	12.157*

† Dunn-Sidák corrected $P \leq 0.10$; * Dunn-Sidák corrected $P \leq 0.05$

Tested but non-significant species:

[1] *Acalypha rhomboidea* (NA), *Aster ericoides* (NP), *Calystegia sepium* (NP), *Daucus carota* (EB), *Erigeron annuus* (NA), *Oxalis stricta* (NP) and *Taraxacum officinale* (EB)

[2] *Acalylpha rhomboidea* (NA), *Aster ericoides* (NP), *Aster lanceolatus* (NB), *Calystegia sepium* (NP), *Erigeron annuus* (NA), *Hieracium caespitosum* (EP), *Oxalis stricta* (NP), *Rumex acetosella* (EP) and *Solanum carolinense* (NP)

[3] *Aster pilosus* (NB), *Daucus carota* (EB), *Euthamia graminifolia* (NP), *Fragaria virginiana* (NP), *Hieracium caespitosum* (EP), *Parthenocissus quinquefolia* (NL), *Poa compressa* (EG), *Rosa multiflora* (ES), *Solidago juncea* (NP) and *Toxicodendron radicans* (NL)

[4] *Euthamia graminifolia* (NP), *Fragaria virginiana* (NP), *Lonicera japonica* (EL), *Oxalis stricta* (NP), *Parthenocissus quinquefolia* (NL), *Rubus allegheniensis* (NS), *Solidago canadensis* (NP), *Solidago rugosa* (NP) and *Toxicodendron radicans* (NL)

Table 2 Results of logistic regression of extinction rates of common species with invasion intensity for four exotic species. Of all the species assessed, only species with significant associations are shown. Extinction rates and invasion intensity were assessed on a plot-by-plot basis for the invasion window selected for each species. Each term is associated with 1 df. Nativity and lifeforms indicated as in Table 1.

Invader	Species	β	Wald χ2
Trifolium pratense[1]	*Ambrosia artemisiifolia* (NA)	0.052	18.993*
Elytrigia repens[2]	---	---	---
Lonicera japonica[3]	*Rumex acetosella* (EP)	0.051	9.973*
Rosa multiflora[4]	*Daucus carota* (EB)	0.016	8.107†
	Oxalis stricta (NP)	0.019	10.069*

†Dunn-Sidák corrected $P \leq 0.10$; * Dunn-Sidák corrected $P \leq 0.05$

Tested but non-significant species:

[1] *Acalyphya rhomboidea* (NA), *Barbarea vulgaris* (EB), *Chenopodium album* (EA), *Digitaria sanguinalis* (EG), *Mollugo verticillata* (EA), *Portulaca oleracea* (EA), *Raphanus raphanistrum* (EA), *Setaria faberii* (EG) and *Verbascum blattaria* (EB)

[2] *Acalypha rhomboidea* (NA), *Ambrosia artemisiifolia* (NA), *Barbarea vulgaris* (EB), *Chenopodium album* (EA), *Digitaria sanguinalis* (EG), *Mollugo verticillata* (EA), *Plantago rugelii* (NP), *Portulaca oleracea* (EA), *Raphanus raphanistrum* (EA), *Setaria faberii* (EG) and *Verbascum blattaria* (EB)

[3] *Acalypha rhomboidea* (NA), *Allium vineale* (EP), *Ambrosia artemisiifolia* (NA), *Aster ericoides* (NP), *Aster pilosus* (NB), *Calystegia sepium* (NP), *Dactylis glomerata* (EG), *Daucus carota* (EB), *Erigeron annuus* (NA), *Plantago lanceolata* (EP), *Plantago rugelii* (NP), *Silene latifolia* (EB) and *Solanum carolinense* (NP)

[4] *Acalypha rhomboidea* (NA), *Ambrosia artemisiifolia* (NA), *Aster ericoides* (NP), *Aster pilosus* (NB), *Calystegia sepium* (NP), *Cerastium vulgatum* (EP), *Erigeron annus* (NA), *Hieracium caespitosum* (EP), *Oenothera biennis* (NB), *Plantago lanceolata* (EP), *Poa pratensis* (EG), *Rumex acetosella* (EP)

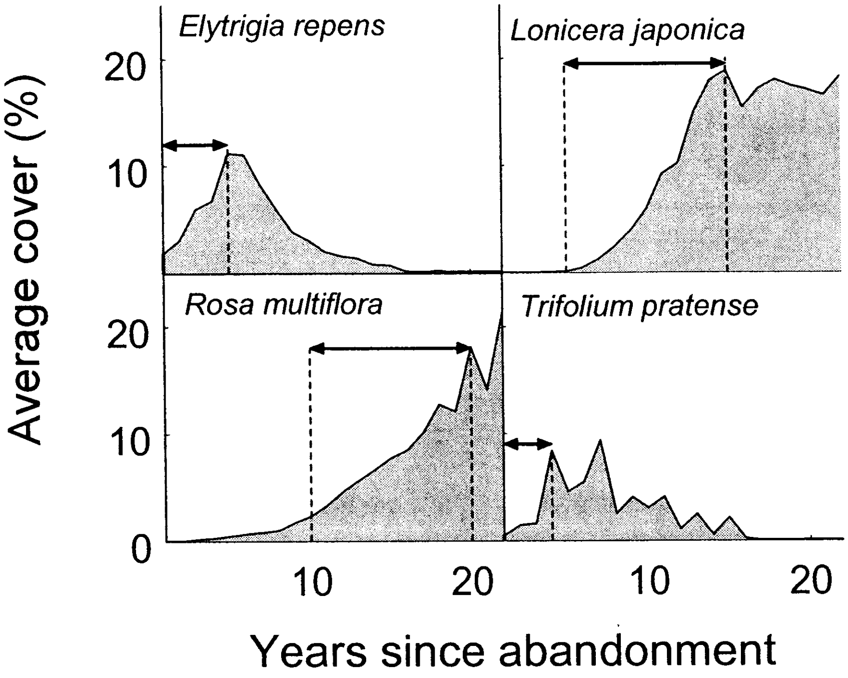

Figure 1 Average plot cover of each invader through time in the Buell-Small Succession Study fields. Times of initial and peak invasion used within the study (invasion window) for each invader are denoted by arrows.

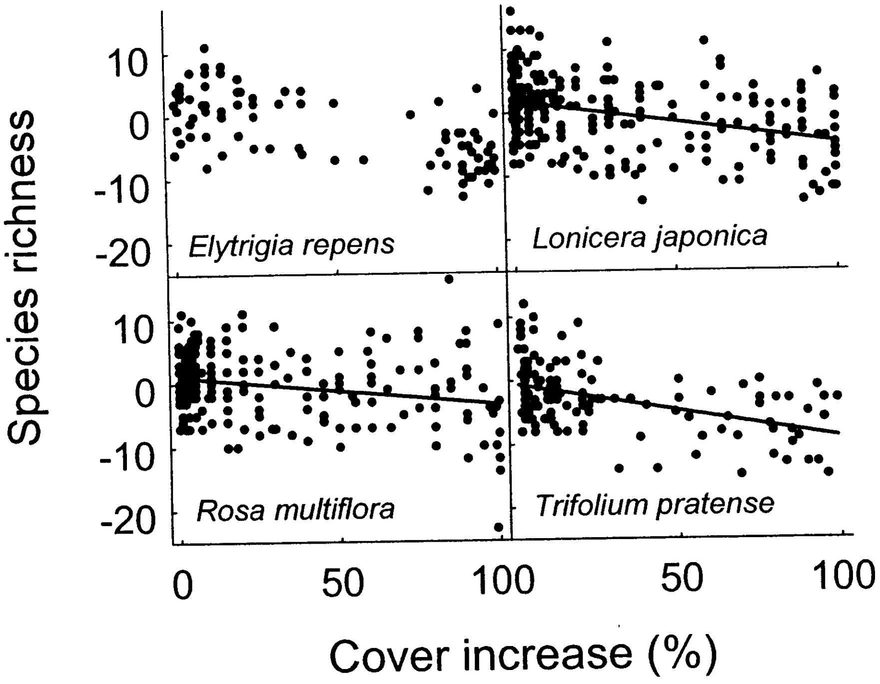

Figure 2 Net change in species richness with increase in invader cover.

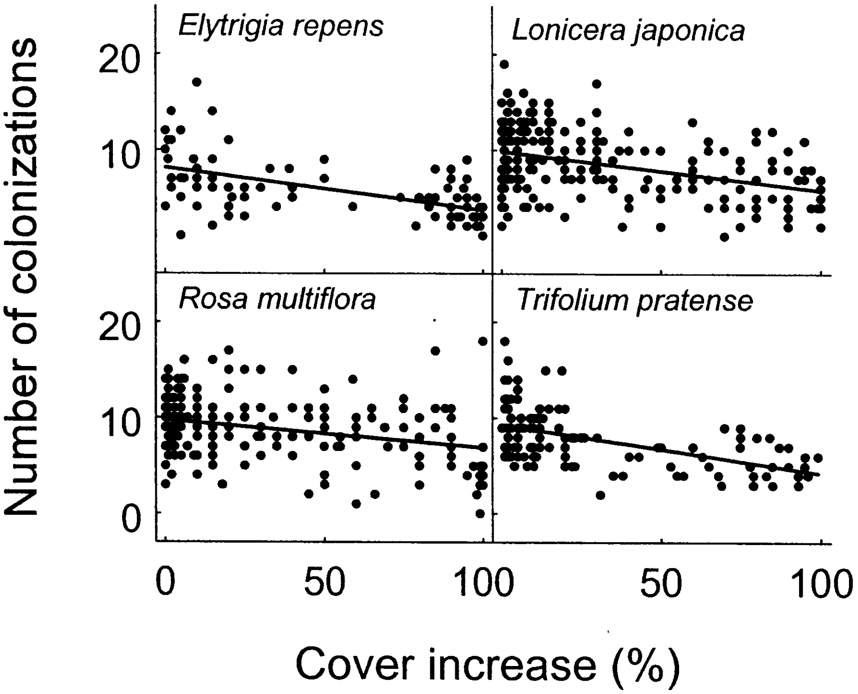

Figure 3 Response of community colonization rates to change in invader cover. Rates calculated as the number of species gained or lost over respective invasion windows.

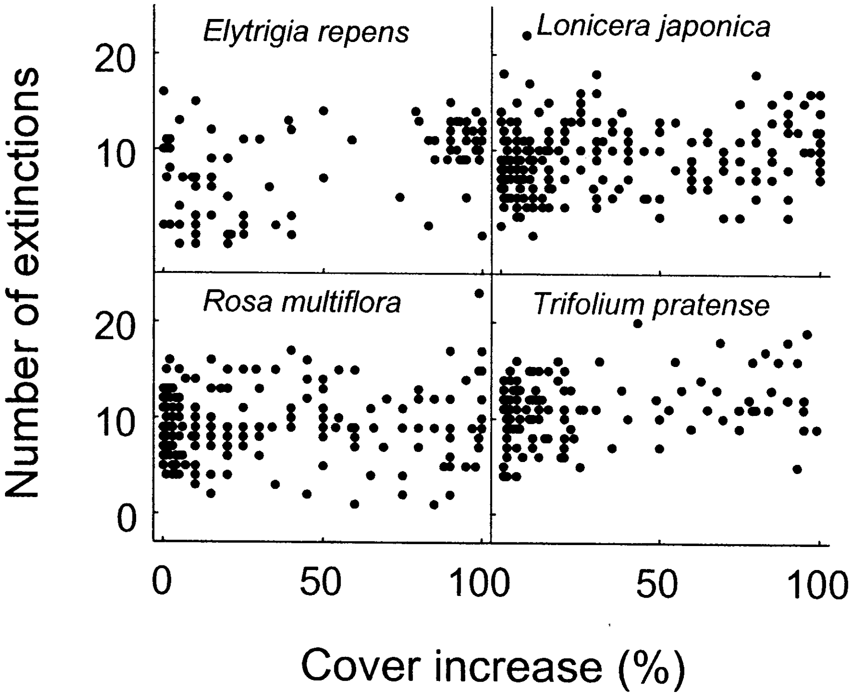

Figure 4 Response of community extinction rates to change in invader cover. Rates calculated as the number of species gained or lost over respective invasion windows.

Discussion

Within this system, field was consistently important but did not confound invasion effects on community dynamics. Field effects on community dynamics most likely reflect legacies from different abandonment regimes and successional trajectories that lead to variation in composition across the site (Myster & Pickett 1990; Meiners *et al.* 2002). Despite variation among fields, I found no field × invasion interactions, suggesting that invasion impacts on community dynamics were consistent across fields.

Neighbourhood responses to invasion

I found consistent impacts across lifeforms of invaders. Invasion of an exotic grass, short-lived perennial, liana and shrub all yielded similar neighborhood responses within this successional system. Neighbourhood species richness declined with increased invasion intensity as a result of decreased colonization rates, suggesting that most invasion impacts occur as new species become established. Although interactions with established resident species appear much less important (Crawley *et al.* 1999; Cahill 2003, Yurkonis & Meiners 2004), this does not rule out species displacement as a mechanism of community-level change. Species such as *Trifolium pratense*, with marginal effects on neighborhood extinction rates and impacts on individual species, may have stronger impacts in other systems.

A variety of environmental and demographic factors may be limiting establishment with invasion. These factors include reductions in light or nutrient availability to levels that inhibit seed germination and establishment (Tilman 1993; Knops *et al.* 1999; Symstad 2000; Cahill 2003; Brandon *et al.* 2004) or the development of thick litter layers that form a barrier to emerging seeds (Facelli & Pickett 1991; Tilman 1993). Reduced colonization rates may also be caused by the saturation of available microsites for establishment by propagules of the invading species (Brown & Fridley 2003). However, several of these factors can be discounted in this system. I did not find abundant seedlings of the invaders (Meiners pers. obs.), suggesting propagule pressure is not influencing colonization dynamics and, with the possible exception of the grass *Elytrigia repens*, the invaders also do not produce a heavy litter layer that would inhibit seed germination (Bosy & Reader 1995). Finally, the common species studied do not appear to be dispersal limited and have the potential to colonize all open microsites (Seabloom *et al.* 2003; Yurkonis & Meiners 2004).

The most probable mechanism of impact is therefore invader control over available resources for colonizing species. Light and soil resource availability (Tilman 1993; Burke & Grime 1996; Knops *et al.* 1999; Davis *et al.* 2000; Cahill 2003; Stevens *et al.* 2004) have been shown to regulate colonization success in many systems. As seedlings would be the demographic stage most susceptible to limiting resources (Fenner 1987), small changes in available resources may dramatically decrease seedling establishment (Crawley *et al.* 1999; Cahill 2003) without affecting mature individuals.

Population responses to invasion

Invasion impacts on population dynamics are similar to those on neighborhood dynamics. Invasion was related to a decline in immigration for 40% of common species, while only 14% showed evidence of displacement with invasion. Although individual species showed displacement effects, these were not strong enough to influence the neighborhood scale pattern. Individual population responses mechanistically explained neighborhood dynamics and showed that the net impacts of an invasion may be generated primarily by establishment limitation rather than extinction (Levins 1969; Ouborg 1993; Blomqvist *et al.* 2003).

One explanation for differences between neighborhood and population dynamics lies in the characteristics of the species that were assessed. Most of the species that exhibited increased extinction rates were short-lived ruderal species whose population dynamics are characterized by high extinction and recolonization rates (Grime 2001). It is possible that, increased extinction rates for such species actually reflect decreased colonization rates within this system. If invasion inhibits resident species recolonization from source populations (rescue effect *sensu* Brown & Kodric-Brown 1977), absence of replacement is likely to lead to increased extinction being observed.

Individual species responses to invasion cannot be understood without assessing potentially obscured invasion impacts. Contrary to the preliminary study, I did not see declines in neighborhood richness with *Elytrigia repens* invasion. However, this invader created significant changes in neighborhood and population colonization rates. In this case, neighborhood and population level effects did not translate into an overall change in species richness. Hence, the lack of a pattern in vegetation may erroneously suggest a lack of impact.

Most studies of invasion impacts do not account for the impacts of several invaders to determine the net effects of invasion on a system, although many systems are challenged with multiple invasions (Simberloff & Von Holle 1999). Within our analyses, I found relationships between multiple invaders and both native and exotic resident species. For example, invasion by each of the early invaders depressed colonization of *Aster pilosus* Willd., a common early successional species. Similarly, colonization rates of *Rumex acetosella* L. were depressed by *Trifolium pratense* while extinction rates were increased by *Lonicera japonica.* Species interacting with multiple invaders would likely experience greater impacts within the system than those affected by only one invasion. Thus, in order to fully assess a resident species' status, invasion studies need to consider the impact of several invaders on resident populations.

I expected invasion to result in stronger effects on species of similar functional characteristics as a result of intense interactions among similar species (Prieur-Richard *et al.* 2000; Symstad 2000; Fargione *et al.* 2003). However, resident species in the same functional group (shrub, liana, etc.) were not disproportionately affected by invasion within this system. For example, *Lonicera japonica* had no effect on the colonization rates of other lianas (*Parthenocissus quinquefolia* (L.) Planchon. and *Toxicodendron radicans* (L.) Kuntze.) and *Rosa multiflora* had no effect on the other common shrub (*Rubus allegheniensis* T. C. Porter.). *Trifolium pratense* reduced colonization of *Aster pilosus* while showing no impacts on *Daucus carota* L. and *Taraxacum officinale* Webber ex. Wiggers., all biennials/short-lived perennials. The one significant interaction does not suggest systematically stronger interactions within functional groups.

An explanation for the lack of strong functional group interactions is that the invader could be colonizing sites unoccupied by the same functional group (Elton 1958; Fox 1987; Mack 2003). However, there is no evidence for this type of control on invasion within this system as invasions of the exotic species discussed here were not regulated by their functional counterparts (Meiners *et al.* 2004) as found by Von Holle &

Simberloff (2004). Differences between our results and those in the literature are most likely attributable to differences in the dynamic nature of this study system. In successional systems species interactions tend to be over shorter periods and resource limitation shifts over time from soil nutrients to light availability (Tilman 1985).

Conclusions

I found a general mechanism for invasion impacts resulting from invader-seedling interactions. This result was consistent across several lifeforms of invaders. I argue that using changes in species richness alone as a method of impact assessment will not adequately predict or describe the effects of invasion. Community level impacts may not reflect important impacts on dynamics of individual species. Furthermore, mitigation efforts must consider that population dynamics do not necessarily translate to community processes and vice versa. If invasion impacts are dominated by establishment limitation, mitigation efforts should be focused on maintaining establishment opportunities for resident species populations. While I specifically focused on the impacts of exotic species in this system, invading species that become dominant in other systems may also show these impacts regardless of nativity.

Invasions must be assessed at both neighborhood and population scales to fully assess impact. However, most studies refrain from this multi-scale approach of invasion and either focus on overall community level effects or individual species competitive responses to invasion (Blossey 1999; Parker *et al.* 1999; Byers *et al.* 2002; Levine *et al.* 2003). Examination of invasion at the former scale may miss significant individual species interactions, while studies at the latter scale cannot determine the effect of the invader on multiple species. I propose this method as a new standard to determine invader impacts on a community by directly linking impacts with the underlying community dynamics that result in altered community structure. Mechanistic approaches such as this are necessary to depict and manage the impacts of invasion and should be applied to other systems to assess the ubiquity of these dynamics in explaining invasion impacts.

CHAPTER 2

DROUGHT IMPACTS AND RECOVERY ARE DRIVEN BY VARIATION IN SPECIES TURNOVER

Abstract

Within communities, species differentially respond to and recover from disturbances that generate impacts on structure and composition at the population and community level. In forest systems, drought acts as a disturbance that may initiate large-scale changes in understory structure and composition while leaving the overstory intact. This study focused on a two-month drought event within an early successional forest system to determine the mechanisms of community response to, and recovery from, drought. Drought induced a 28% decline in species richness and cover as a result of decreased colonization rates and increased extinction rates. However, the community quickly recovered via increased colonization following drought. Drought had little long-term effect on community structure (species richness and cover) and did not generate large-scale compositional shifts across the community. Within sites, drought resulted in subtle changes in the composition of the understory community. Ruderal (annual and biennial) species were more likely to increase or decrease in cover and frequency than the more stress tolerant perennial and woody species. Increased extinction and decreased colonization appear to be general mechanisms driving drought impacts while recolonization appears to be the primary mechanism driving community recovery. Although drought impacts and recovery appeared to be predictable at the community level, population responses to drought were rather unpredictable. Population dynamics appear to be generally driven by species turnover within sites and not by large-scale shifts

in species performance. These common causal mechanisms should be explored in other systems to determine the extent of their generality in determining drought impacts on community dynamics.

Introduction

Communities often experience disturbances that vary along a gradient in intensity and frequency (Connell 1978). Disturbances such as fire and drought can be a common feature of communities that is necessary for maintaining community structure and composition (Leitner *et al.* 1991; Hanson & Weltzin 2000; Turner *et al.* 2003). These disturbances can also function as mechanisms of community change, altering community structure and composition (Tilman & El Haddi 1992; Allen & Breshears 1998; Condit 1998; Larsen & MacDonald 1998; Scheffer *et al.* 2001; Delissio & Primack 2003). Although the role of disturbance may vary among communities, disturbance impacts at the community level result from the net responses of individual species to the perturbation (Pickett & Cadenasso 2005). Thus in order to fully understand disturbance controls over a system one must consider both community and population responses to disturbance.

In many systems, drought acts as a disturbance that may initiate large-scale changes in community structure and composition (Tilman & El Haddi 1992; Allen & Breshears 1998; Condit 1998; Scheffer *et al.* 2001; Delissio & Primack 2003). Drought generally results in decreased productivity, diversity and establishment, increased rates of mortality and litter accumulation, and altered nutrient cycling in the community (Bollinger *et al.* 1990; Tilman & El Haddi 1992; Condit *et al.* 1995; Sternberg et al. 1999; Delissio & Primack 2003; O'Neill *et al.* 2003; reviewed in Hanson & Weltzin 2000). Drought impacts have been largely studied in grasslands (e.g. Tilman & El Haddi 1992; Sternberg *et al.* 1999; Knapp *et al.* 2002; Morecroft *et al.* 2004; Stampfli & Zeiter 2004) or tropical forests (e.g. Condit *et al.* 1995; Laurance *et al.* 2001; Delissio &

Primack 2003). However, there have been relatively few mechanistic studies of the community and population level effects of drought (Hanson & Weltzin 2000) particularly in deciduous forest understory communities (Roberts & Gilliam 2003).

The main mechanism by which communities change with disturbances such as drought is through changes in the rate of species turnover. At any time, species richness is a balance of local colonization and extinction rates within a site (MacArthur & Wilson 1967). Thus, any changes in structure reflect altered colonization and/or extinction rates within a community and this conceptual framework can be used to determine the mechanisms of community change in response to drought.

Decreased community colonization rates indicate that species establishment is limited within the system during drought (Sternberg *et al.* 1999). Reduced establishment is expected to occur during drought because of seedlings' high susceptibility to low soil moisture. Because of their small root systems seedlings are unable to procure water from deep soil zones and are typically unable to establish during dry periods (Fenner 1987), which can have lasting effects on future community composition (Delisso & Primack 2003).

Increased community extinction rates indicate that species mortality is occurring in the system during drought (Tilman & El Haddi 1992; Bartha *et al.* 2003). Mortality is expected to occur during drought because some species do not possess adaptations for surviving in stressful environments. Ruderal species, with little stress tolerance, tend to be quickly eliminated by drought (Grime 1991; Tilman & El Haddi 1992), while perennial and deep-rooted species tend to perform better during drought (Grime 1991; Tilman & El Haddi 1992; Morecroft *et al.* 2004) even though their growth may be dramatically reduced (Buell *et al.* 1961). In addition to variation among lifeforms, species within a community probably vary in their drought tolerance due to variation in life history traits and physiological adaptations, resulting in a gradient of species' drought response among (Condit *et al.* 1995).

The mechanisms driving community recovery following a disturbance are quite similar to those driving impacts. Following drought, colonization is important for re-establishing community structure and composition (Bartha *et al.* 2003; Stampfli & Zeiter 2004). Drought can open a temporal colonization window where new species enter the community as a result of resource fluctuation and reduction in competition intensity (Grime *et al.* 1994; Davis & Pelsor 2001; Bartha *et al.* 2003). Colonization during this time can lead to important transitions in community composition that may persist long after the disturbance (Davis *et al.* 2000; Bartha *et al.* 2003). In addition to increased colonization rates, extinction rates may be reduced during recovery periods due to lowered competitive interactions among species (Grime *et al.* 1994; Coomes & Grubb 2000).

While community dynamics are determined by species dynamics across an entire site, it is unclear how species respond to site heterogeneity (Hanson & Weltzin 2000). Drought can affect individual species within the community in one of two ways. A species may be either affected uniformly across a site or may show local variation. If a species was affected uniformly across a site by drought, extinction and colonization dynamics would be expected to be similar regardless of site identity or history. Uniform impacts across a site would lead to directional shifts in community composition and/or structure with drought (Scheffer *et al.* 2001). On the other hand, if local characteristics largely determine drought impact and recovery, colonization and extinction dynamics would be expected to vary within a site. In this case recovery within any neighborhood would be stochastic based on resident species drought tolerance, local seed bank composition, and local propagule inputs (Grubb 1988; Dalling *et al.* 1998; Roberts & Gilliam 2003).

This study focuses on the impact of a severe drought within an early successional forest system to determine the mechanisms of community response and recovery to disturbance. I specifically addressed 1) How does drought affect species turnover dynamics and community structure?, 2) How variable are drought impacts within a site and among species?, 3) How does drought differentially impact species?, 4) What are the mechanisms and speed of community recovery from drought?, and 5) Does drought have persistent effects on community structure?

Methods

Study System

To assess drought impacts on community structure and composition, I used data collected from abandoned agricultural land in the Piedmont region of New Jersey, USA (40°30' N, 74°34' W) as part of the Buell-Small Succession Study (BSS). Initiated in 1958, the study consists of 10 agricultural fields abandoned in pairs over a period of 8 years located at the William L. Hutcheson Memorial Forest Center near East Millstone, NJ (Buell *et al.* 1971; Pickett 1982). Fields are distributed across a fairly level site with uniform silt loam soils (Ugolini 1964). Fields differed in season of abandonment, last crop and final plowing regime to assess the impact of different disturbance legacies on succession (Myster & Pickett 1990). Within each field, 48 permanently-marked 0.5 × 2.0 m plots were established immediately after abandonment (Pickett 1982). In alternate years, five of the fields were sampled and the percent cover of all species present in each plot was recorded. These data represent the longest continuous data set on post-agricultural successional change known.

I used data collected from 5 non-adjacent fields (C5, C7, D1, D3 and E2) that were sampled during a severe drought in 1999. An additional sampling was conducted during 2000 to capture post-drought recovery. Despite variation in pre-abandonment conditions, the general successional trajectories of all fields were remarkably similar, though composition often varied, as did the rate of successional change (Myster & Pickett 1990, 1994). Fields were predominantly forested with an herbaceous understory in the period used for this study. *Acer* and *Quercus* species dominated the canopy in the C and D fields while *Juniperius virginana* L. dominated the canopy in field E2. Due to the presence of overlapping plant canopies (tree, shrub and herbaceous) cover often exceeded 100% within each plot. Nomenclature follows Gleason & Cronquist (1991).

I used monthly rainfall data from the New Brunswick, New Jersey 3SE weather station (# 286055; 40°28' N, 74°26' W, elev. 26.2m) located 12 km east of the BSS site (NCDC Annual Climatological Summary, NOAA). As the vegetation was sampled in July of each year, growing season rainfall was defined as the total rainfall from May to July. While technically still the growing season, rainfall occurring in August/September would not affect vegetation at the time of data collection. The mean growing season rainfall from 1958 to 2003 was 327mm. Rainfall data were calculated as percent departure from normal growing season rainfall (1958-2003) for each year (Fig. 5a). From 1997 to 2003 growing season rainfall deviation ranged from +41% (460mm) in 2003 to -47% (173mm) during the 1999 drought. In June and July of 1999, the area received approximately 30% of the normal monthly rainfall. However, annual rainfall for 1999 was above normal due to landfall of hurricane Floyd in August (Fig. 5b). The drought resulted in standing dead vegetation at the time of sampling and a marked thinning of the tree canopy (S.J. Meiners pers comm).

To determine the mechanism(s) that generate the 1999 drought impacts within this early successional forest analyses were conducted at two ecological scales, neighborhood and population. The neighborhood scale, hereafter defined as the local community within each plot, is the scale at which species interact to generate drought impacts. The neighborhood scale was used to assess drought impacts on species richness, cover, colonization rates and extinction rates. Population (species) scale analyses were used to determine the mechanism(s) responsible for neighborhood level dynamics. At the population scale, I examined individual resident species responses to and recovery from drought based on their plot abundance.

Neighborhood dynamics

To address neighborhood (plot) level drought impacts, I calculated plot species richness, total cover, colonization, and extinction rates during each sample year from 1997 to 2003. Colonization rate was defined as the number of species not present in the previous sample year in each plot. Likewise, extinction rate was quantified as the number of species lost from one sample year to the next in each plot. Repeated Measures ANOVA (RMANOVA; SPSS Inc, Chicago, IL) was used to assess changes in species turnover through time. Contrasts were used to specifically compare drought impacts and post-drought recovery to pre-drought conditions (SPSS Inc, Chicago, IL).

Population dynamics

To determine drought impacts on individual species dynamics, I calculated cover for a suite of common species that responded to the drought. Species were selected to have a total pre-drought cover >800% when species cover was summed across all plots in the five fields (mean plot cover >3.3%) and to have lost >50% of their cover across the site from 1997 to 1999. Abundance of each of the six species that met these criteria was then related to time using RMANOVA and contrasts were used to compare drought and post-drought cover to pre-drought abundances.

Community recovery after drought

To determine if drought had lasting impacts on community structure I determined plot species richness before (1997) and after (2001) the 1999 drought. Because most of the common species did not recover until 2001, these data were used as post-drought measures. Within each field, plot species richness before and after drought was correlated using Spearman correlation.

To assess if overall community composition changed with drought, species cover and frequency across all fields were analyzed before and after drought. Species were divided among three lifeform groups and analyzed separately. Lifeform groups consisted of ruderal (annual and biennial), perennial and woody (tree, shrub and liana) species. Spearman correlation was used to relate individual species cover and frequency before (1997) and after (2001) drought across all five fields. Species that went extinct or colonized the site after 1997 are not included in this analysis to allow log transformation of the data.

Results

Neighborhood dynamics

Fields differed dramatically in the intensity of drought impact and rate of recovery. In all RMANOVA analyses with neighborhood level metrics (species richness, cover, colonization and extinction rate) field was significant and year × field interactions occurred (Table 3). Although all neighborhood metrics changed with drought, some fields had greater changes than others. For example, plots in field E2 lost twice as many species (37% decline in species richness) as plots in field D1 (16% decline) during the drought. In field D3, the extinction rate dropped by 21% while it increased by 50% in E2.

Despite differences among fields, species richness and cover declined by approximately 28% during the drought from pre-disturbance conditions ($P < 0.001$; contrast with 1997; Fig. 6a,b) and returned to pre-drought conditions by 2000. Cover significantly exceeded pre-drought conditions in 2001 by 5% ($P = 0.037$; contrast with 1997; Fig. 6a,b) and species richness exceeded 1997 values in 2003 by 13% ($P < 0.001$; contrast with 1997; Fig. 6a,b).

Declines in species richness and cover resulted from changes in species turnover rates with the drought. Despite individual field and field × year effects, colonization rates decreased by 33% and extinction rates increased by 13% during the drought (Table 3, Fig. 6c,d) resulting in the net loss of richness. Species richness recovered to pre-drought levels by 2000 through elevated colonization and decreased extinction rates. Colonization rates returned to pre-drought conditions by 2001, but increased again in

2003, a relatively wet year. However, extinction rates did not recover following the drought, remaining below pre-drought rates through 2003.

Population dynamics

Cover of individual common species varied among fields and showed different temporal patterns (Table 4, Fig. 7). Although all species tested were abundant across the site (>800% total cover), they varied dramatically in abundance among fields. Some fields contained high cover of the species while they were virtually absent in other fields, as was most evident for *Eupatorium rugosum* Houttuyn., *Solidago rugosa* Miller and *Toxicodendron radicans* (L.) Kuntze.

In addition to variance among fields in absolute abundance, species also varied in drought response among fields (a field × year interaction). Individual species in some fields showed no drought impacts, while in other fields there were dramatic declines in cover. For example, *Toxicodendron radicans* cover dropped in field D3 by 58% but remained relatively unchanged (3% increase) in field D1. Post-drought recovery dynamics of species also varied among fields. Interestingly, there was a burst of cover and increase in frequency of the exotic species *Alliaria petiolata* (Bieb.) Cavara & Grande immediately following the drought in field C7, increasing from 9% in 1997 to 44% mean plot cover in 2000. However, *A. petiolata* cover returned to essentially pre-drought levels in subsequent years. The only species that showed consistent response and recovery across fields was the liana *Parthenocissus quinquefolia* (L.) Planchon that had no field × year interaction (Table 4). This species declined in cover by 77% with drought and then increased in all fields until 2003.

Despite differing population dynamics among fields, all six species declined in total cover across the site (summed across fields) during the drought and generally returned to pre-drought abundances within two years. Immediately following the drought (2000), *Poa compressa* L. and *Alliaria petiolata* cover returned to pre-drought conditions, while abundance returned to pre-drought conditions for half of the species (*Eupatorium rugosum*, *Parthenocissus quinquefolia* & *Toxicodendron radicans*) the second year after drought (2001). The only species that did not recover pre-drought abundances was *Solidago rugosa*, a perennial characteristic of earlier successional stages. Mean plot cover in this species decreased by 80% across the site in 1999 and remained below 1997 abundances in all fields despite some recovery in more open microsites.

Community recovery after drought

The 1999 drought did not result in dramatically altered community structure. Despite decreases in plot species richness in 1999, mean plot richness recovered to pre-drought levels in 2001 (Fig. 6). Individual plot species richness after drought (2001) was positively correlated to plot richness before drought for all fields (1997) (Table 5, Fig. 8). Sixty percent of all plots had average post-drought species richness within 10% of pre-drought richness, while 23% of all plots gained and 17% lost more than 10% of pre-drought richness.

After drought, species generally returned to pre-drought abundances and frequency across the site (Table 6, Fig. 9). However, common species were less likely to have dramatic changes in distribution and abundance than infrequent species. In addition, species recovery varied with lifeform. Woody species tended to change the least while annual species showed the greatest changes across the drought (Table 6, Fig. 9). However, woody stem density decreased by approximately 20% from 1997 to 1999 and did not recover until 2003. The most dramatic increase in cover and frequency occurred with the exotic annual *Microstegium vimineum* (Trin.) A. Camus, which increased in total cover from 0.1% in 1997 to 646.6% in 2001.

Table 3 Effects of the 1999 drought on species richness, cover, colonization and extinction. Between and within subject effects are listed. Within subject F test comes from Pillai's Trace.

Model term	hypothesis df /error df	F	*P*
Species Richness			
Field	4/235	9.859	**<0.001**
Year	4/232	92.001	**<0.001**
Year × Field	16/940	4.416	**<0.001**
Cover			
Field	4/235	12.010	**<0.001**
Year	4/232	70.658	**<0.001**
Year × field	16/940	3.372	**<0.001**
Colonization			
Field	4/235	10.182	**<0.001**
Year	4/232	45.762	**<0.001**
Year × Field	16/940	3.092	**<0.001**
Extinction			
Field	4/235	7.856	**<0.001**
Year	4/232	96.793	**<0.001**
Year × Field	16/940	4.630	**<0.001**

Table 4 Effects of drought on the cover of common drought susceptible species through time. Species with >800% cover summed across all plots in 1997 and that lost >50% total cover in 1999 are shown. Within subject F-test comes from Pillai's Trace.

Species	hypothesis df /error df	F	*P*
Alliaria petiolata			
Field	4/235	17.916	**<0.001**
Year	4/232	36.115	**<0.001**
Year × Field	16/940	14.624	**<0.001**
Eupatorium rugosum			
Field	4/235	28.073	**<0.001**
Year	4/232	29.371	**<0.001**
Year × field	16/940	6.739	**<0.001**
Parthenocissus quinquefolia			
Field	4/235	5.030	**0.001**
Year	4/232	13.306	**<0.001**
Year × Field	16/940	1.170	0.286
Poa compressa			
Field	4/235	4.183	**0.003**
Year	4/232	3.971	**0.004**
Year × Field	16/940	1.997	**0.011**
Solidago rugosa			
Field	4/235	7.668	**<0.001**
Year	4/232	10.359	**<0.001**
Year × Field	16/940	2.241	**0.003**
Toxicodendron radicans			
Field	4/235	7.022	**<0.001**
Year	4/232	6.995	**<0.001**
Year × Field	16/940	2.471	**0.001**

Table 5 Relationship between plot species richness before (1997) and after (2001) the 1999 drought. Data presented are Spearman correlation coefficients.

Field	N	R	P
All fields	240	0.598	**<0.001**
C5	48	0.669	**<0.001**
C7	48	0.683	**<0.001**
D1	48	0.466	**0.001**
D3	48	0.704	**<0.001**
E2	48	0.419	**<0.001**

Table 6 Relationship between species abundance and frequency before (1997) and after (2001) the 1999 drought. Species were divided among three lifeform groups: ruderal (annuals and biennials), perennial and woody (trees, shrubs and lianas). Data presented are Spearman correlation coefficients.

Lifeform group	N	Cover		Frequency	
		R	P	R	P
Ruderal	26	0.409	**0.038**	0.598	**0.001**
Perennial	47	0.731	**<0.001**	0.798	**<0.001**
Woody	47	0.777	**<0.001**	0.846	**<0.001**

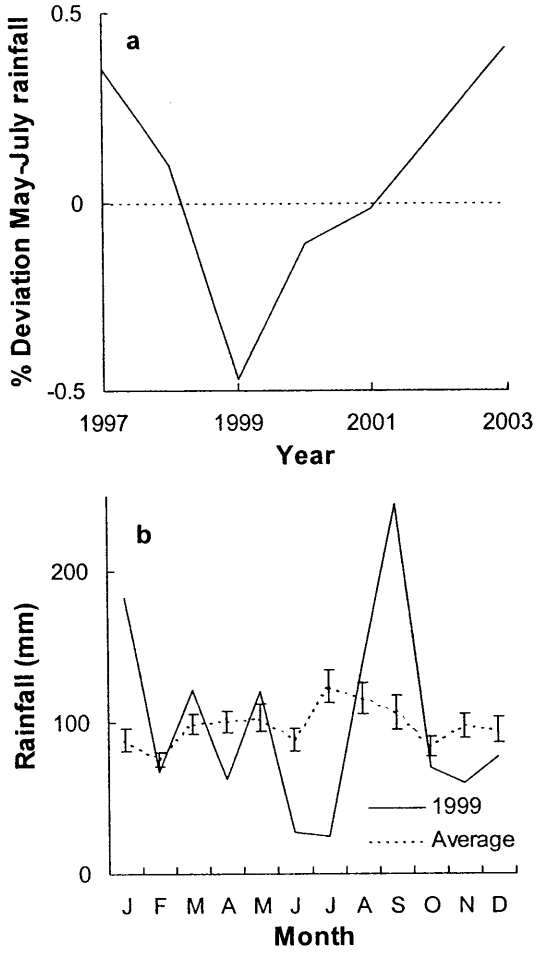

Figure 5 Growing season (1997 to 2003) and 1999 monthly rainfall data from the New Brunswick, NJ weather station. Data are summarized as deviation from normal (1958-2003) of total growing season (May to July) rainfall (a) and total monthly rainfall (mm) during 1999 (b). Elevated rainfall in August of 1999 is due to landfall of hurricane Floyd.

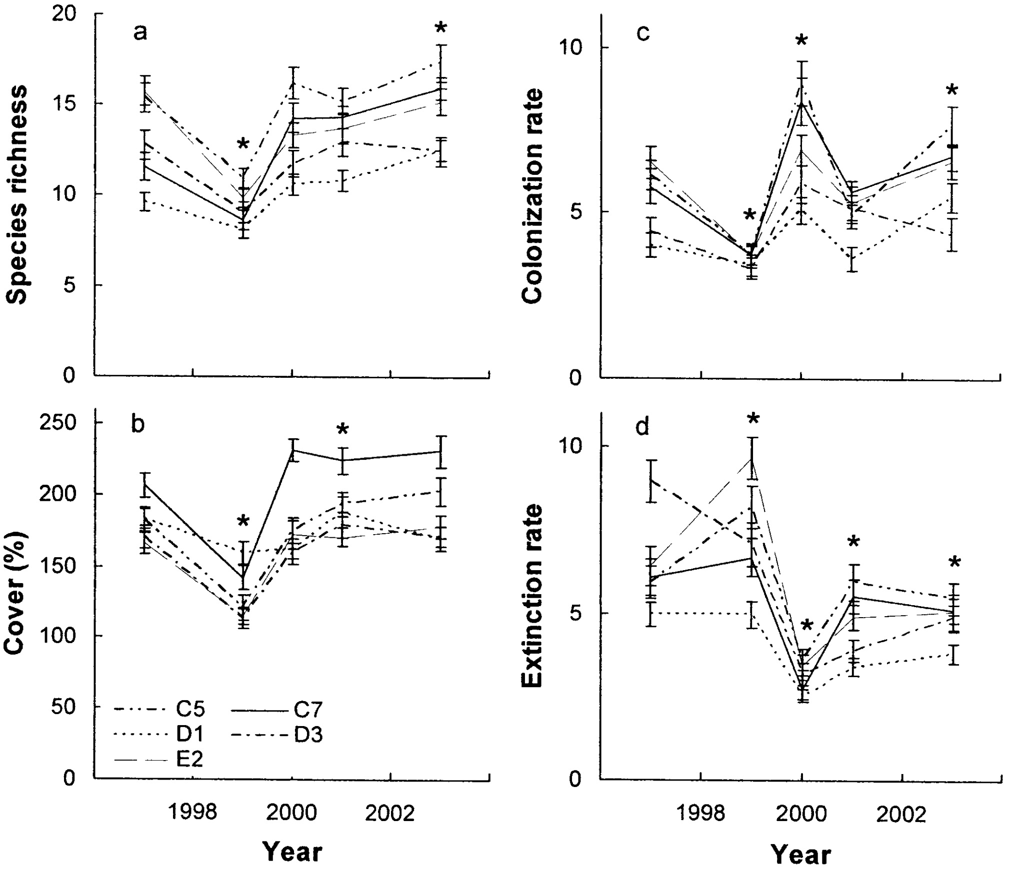

Figure 6 Change in species richness, cover and species turnover through time. Average plot data are summarized within each of five non-adjacent fields that differ in their respective disturbance history. Significant contrasts (P<0.05) with pre-drought levels across all fields are indicated by an asterisk. Bars represent ± 1 standard error of the mean.

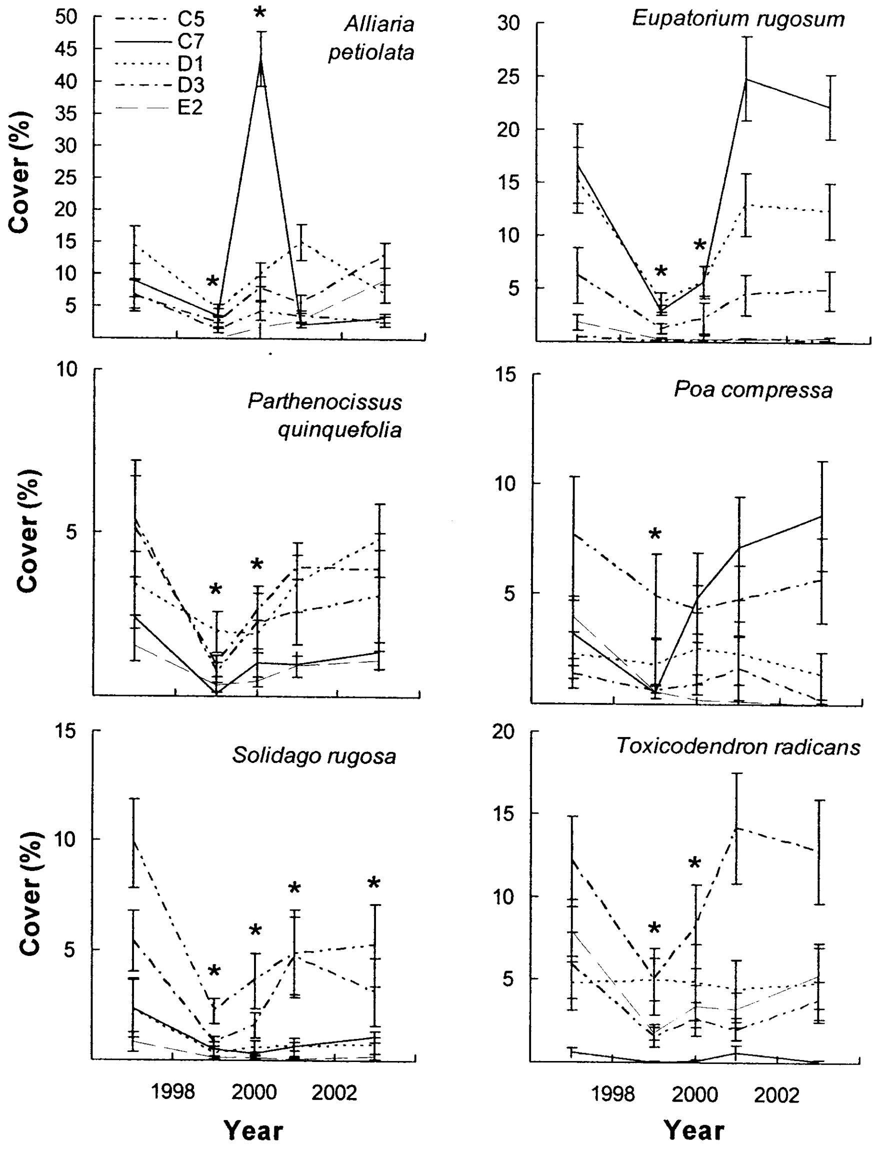

Figure 7 Common species responses to a 1999 drought. *Alliaria petiolata* is an exotic biennial, *Poa compressa* is an exotic perennial grass, *Eupatorium rugosum* and *Solidago rugosa* are native perennial forbs and *Parthenocissus quinquefolia* and *Toxicodendron radicans* are native lianas. Data are graphed as the mean plot cover per field ± 1 standard error. Significant contrasts (P <0.05) with pre-drought (1997) abundance across all fields are indicated by asterisks.

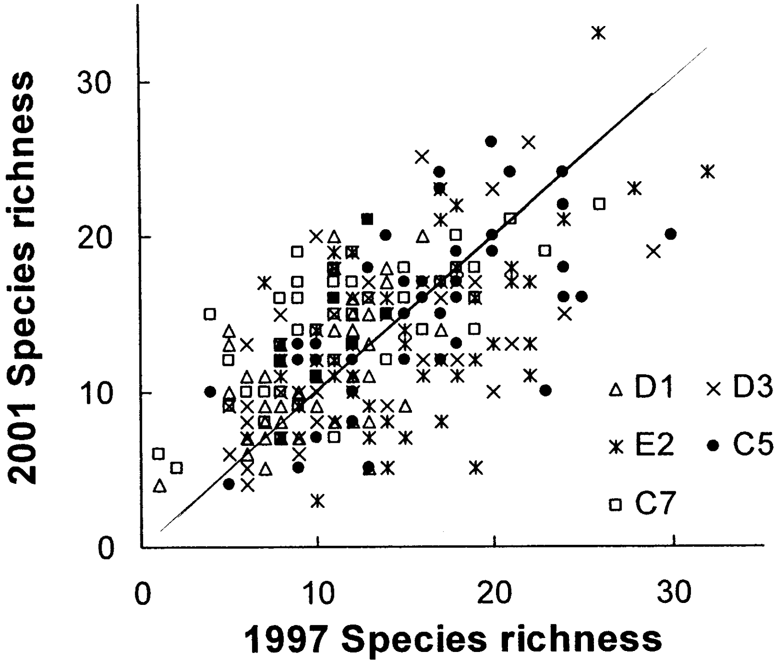

Figure 8 Plot species richness before and after a 1999 drought. Plots within each of five non-adjacent fields are differentiated with unique symbols. A one to one reference line has been added to indicate no change.

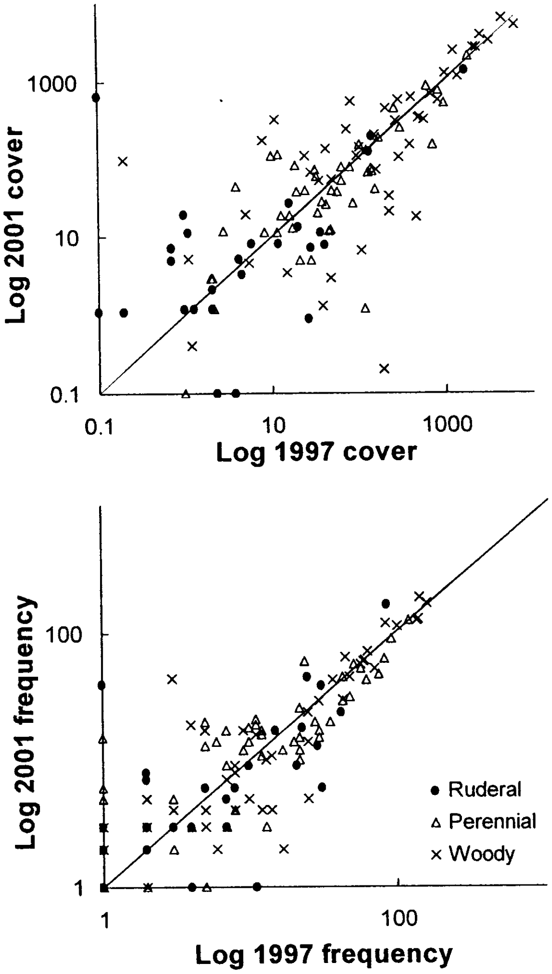

Figure 9 Community composition before and after a 1999 drought. a) cover of each species in the community totaled across all fields, b) frequency of each species in the community totaled across all fields. Species are divided into three lifeform categories: ruderal (annual and biennial), perennial and woody (trees, shrubs and lianas). One to one lines have been added for reference.

Discussion

Overall, this early successional forest community changed dramatically in response to a two-month drought but quickly recovered with few lasting effects. One of the most common drought effects was that fields within the study site responded differently to the drought and followed different recovery paths. Fields differed in their disturbance history (plowing, crop, season and year of abandonment), which led differences in the initial assembly of species and subsequent successional trajectories (Myster & Pickett 1990, 1994). Thus, variation in disturbance history and species assemblages across the site appears to have a strong effect on local drought response and recovery.

Neighborhood dynamics

Response- Neighborhood species richness and cover declined by approximately 28% with drought as a result of both decreased colonization and increased extinction rates. Colonization rates would have declined as opportunities for establishment and/or germination became limited within the system during the drought (Sternberg *et al.* 1999). Seedlings with developing root systems would be more susceptible to mortality regardless of their ability as mature plants to deal with drought (Fenner 1987). Within forested systems, where tree seedling establishment is often controlled by soil moisture (Osmand *et al.* 1987), decreased seedling recruitment has been indicated as a major factor in community change associated with drought (Delissio & Primack, 2003). Within this system, tree seedling establishment decreased by approximately 20% with drought (Yurkonis unpublished data). These effects may also translate to the herbaceous understory community where recruitment can be limited by soil water availability (Anderson *et al.* 1968).

Local extinction during drought increased as a result of mortality of individuals that could not tolerate low soil moisture (Grime 1991; Tilman & El Haddi 1992; Condit *et al.* 1995). Drought appeared to differentially affect ruderal species that have limited storage of nutrients and shallow root systems (Grime 1991). Established species that should have deep root systems (Tilman & El Haddi 1992; Morecroft *et al.* 2004) or carbohydrate stores (e.g. woody species) were not as dramatically affected by drought (Grime 1991). Although during severe or prolonged droughts mortality can occur in established tree and shrubs (Condit *et al.* 1995), this does not appear to have happened in this system as established woody species did not change appreciably in frequency or abundance as a result of the drought.

Recovery- Although dramatically impacted by drought, neighborhood species richness and cover returned to pre-drought levels within one year. This suggests that neighborhood structure within this system is fairly resistant to environmental perturbation and did not experience any sort of catastrophic shifts (Duffy & Meier 1992; Scheffer *et al.* 2001). Plots regained species richness via recolonization after the drought (Stampfli & Zeiter 2004). Colonization rates following the 1999 drought were higher than pre-drought levels. This increase probably occurred as microsites that remained uncolonized or were created by the drought were colonized by propagules from the seed bank or from species that reproduced during the drought (Grubb 1988; Grime *et al.* 1994). In addition, establishing seedlings may benefit from decreased competition with recovering resident species (Grime *et al.* 1994; Bartha *et al.* 2003).

Drought induced a colonization window within this system that led to relatively small compositional changes in the community. As cover dropped and extinction increased with drought, microsites were presumably opened both above and belowground (Coomes & Grubb 2000; Casper *et al.* 2003). In the following year, the community experienced a burst of colonization as species utilized excess resources in the community within these empty sites (Sternberg *et al.* 1999; Davis *et al.* 2000; but see Walker *et al.* 2005). As a result of this influx of colonization, species richness and cover quickly returned to pre-drought levels. The colonization window opened by drought also served as an opportunity for species invasion and marked a subtle transition in local species assemblages without affecting community structure (Sternberg *et al.* 1999; Davis *et al.* 2000; Bartha *et al.* 2003).

The colonization window opened by drought facilitated local expansion of native and exotic species within this system. *Alliaria petiolata* increased in frequency and cover in field C7, without corresponding increases in the remaining fields. Furthermore, both native and exotic ruderal species tended to increase in cover and frequency across the site as the system recovered from drought. Other, more open, areas of the Hutcheson Memorial Forest Center had large increases in species that germinated in late fall or early spring and established the following summer (e.g. *Barbarea vulgaris* R. Br., *Chrysanthemum leucanthemum* L. and various grasses) corresponding with the colonization window opened by the 1999 drought (E. Tulloss & S.J. Meiners, unpublished data). Establishment of these ruderal species in the colonization window may have been accelerated by high rainfall in August of 1999.

As neighborhood species richness returned to pre-drought levels, extinction rates remained below pre-drought conditions through 2003. Extinction rates remained low, as species that reestablished during the colonization window probably experienced decreased competition from resident species that had not yet returned to pre-drought abundances (Grime *et al.* 1994, Bartha *et al.* 2003). However, once perennial resident species recover and begin to competitively exclude more transient species, extinction rates would be expected to return to pre-drought levels.

Population dynamics

Despite general declines in abundance with drought, population dynamics appear to be more strongly determined by local conditions than by individual drought tolerance traits (Roberts & Gilliam 2003; Jongejans & de Kroon In press). Individual species' dynamics varied greatly among fields during and following drought. *Toxicodendron radicans* cover stayed relatively constant in field D3, but declined in cover by 58% in field D1. *Solidago rugosa*, a species characteristic of open areas, had an 80% decline in total cover and did not return pre-drought abundances across the site despite recovery in individual fields. Although such changes in cover can reflect variation in productivity of individual plants, dramatic declines in cover probably also reflect overall changes in the number of individuals. The 1999 drought resulted in standing dead vegetation at the time of sampling (S.J. Meiners pers comm) indicating that some direct mortality resulted from the drought. Therefore, declines in average cover within a field likely correspond to net decreases in neighborhood colonization and increases in neighborhood extinction rates for each species.

On a finer spatial scale, variation within individual species' responses may reflect differences in microsite composition that may alter drought impact. Some species may alleviate drought impacts on others by increasing local soil moisture via hydraulic lift (*e.g. Acer saccharum,* Dawson 1993). Tree seedling mortality is strongly dependent on the previous season's growth (Kobe & Coates, 1997). Therefore, seedlings experiencing competition would be expected to exhibit higher mortality during the drought. Mortality would also be expected to increase with species that are growing in low resource environments, undergoing intense herbivory or are diseased prior to the drought (Hanson & Weltzin 2000). In addition, species turnover is also influenced by the seed bank and local seed production (Dalling *et al.* 1998, Roberts & Gilliam 2003), which determines the species that colonize empty microsites. This variation in neighborhood composition would lead to the observed variation in species' responses. The varied composition among fields due to their different history would also alter microsite conditions leading to the observed variation in drought response among fields. These results support a more view of species drought responses and community dynamics in general (Dalling *et al.* 1998).

Community recovery after drought

Despite dramatic drought impacts, this system regained pre-drought community structure quickly after disturbance. Species richness returned to pre-drought levels and richness prior to drought was strongly correlated with richness after recovery. Furthermore, species abundance and frequency returned to approximately the same pre-drought levels for most common species.

While there were few persistent impacts of the drought on community structure, transitions in local composition may have long-term indirect effects on community composition. The exotic annual *Microstegium vimineum* increased in both cover and frequency after the drought. The drought may have facilitated *M. vimineum* establishment through increased light penetration through the canopy (Cole & Weltzin 2005), though this species was invading prior to the drought from the adjacent old-growth forest. Since the drought, *M. vimineum* has increased in cover and frequency across the site and has become a dominant understory species (Yurkonis pers. obs.).

Conclusions

Within this early successional forest, a two-month drought acted as a mechanism of community change by changing community dynamics and species composition without altering overall community structure. Species varied dramatically in their responses to drought and showed stochastic responses across fields (Davison & Forman 1982; Dalling *et al.* 1998; Beatty 2003). Population dynamics appeared to be a function of local conditions, which can be influenced by local dominant species, competitive interactions, dispersal and the local seed bank (Roberts & Gilliam 2003). Finally, changes in community composition with drought may have left a persistent legacy due to species invasion (Davis *et al.* 2000; Bartha *et al.* 2003).

My results suggest that increased extinction and decreased colonization are general mechanisms driving drought impacts, while recolonization appears to drive community recovery. Although drought impacts and recovery appeared to be predictable at the community level, population responses to drought were rather unpredictable, driven by neighborhood species turnover not large-scale shifts in species abundance. While a more severe drought may have had greater, more persistent impacts, the mechanisms of community change should be similar. The common causal mechanisms of community change presented here should be explored in other systems to determine the extent of their generality in driving drought impacts on communities.

CONCLUDING REMARKS

The conceptual framework of species turnover dynamics has proven useful in determining the mechanisms of community change within the study system. Analysis of two disturbance scenarios has lead to the characterization of the general mechanisms driving community change. In both scenarios the mechanisms of community change are quite similar. Exotic species invasion generally results in establishment limitation for other species. Although vegetation change from drought resulted from both mortality and establishment limitation, recovery from drought is driven by re-colonization during persistent conditions of low mortality and competition. Thus, overall results suggest that community response to disturbance is primarily driven by colonization dynamics.

Mechanisms of exotic species impacts

Exotic species invasion resulted in declines in diversity caused by reduced colonization rates, and not increased extinction rates for all invaders. Invasion prevented seedlings from becoming established but did not result in displacement of resident species. These findings were also supported at the population scale where invasion prevented establishment of numerous species and resulted in limited species displacement. Furthermore, invasion impacts were essentially the same for all invaders regardless of lifeform, suggesting that establishment limitation may be a general mechanism of invasion impacts. Future researchers should investigate the generality of establishment limitation as the mechanism of invasion impact. If this is a general phenomenon, then increasing establishment of native species through actions such as transplanting adult native species should be a goal for mitigating exotic species impacts.

Mechanisms of community response to drought

During drought, diversity and cover declined due to reduced colonization and increased extinction rates. In this case, both establishment limitation and mortality were general mechanisms of community change. Species varied in their response to drought and showed significant variation among fields. At the population level, ruderal species were most strongly affected by drought, showing the greatest increases and decreases in abundance and frequency. Despite dramatic declines with drought, species quickly returned to the system within a colonization window opened by drought. Interestingly, drought had little long-term effect on community structure and initiated only subtle changes in the understory community composition. These results suggest that plant community composition responds stochastically to drought without overall changes in structure. If this is a general phenomenon then future drought effects can be mitigated with a focus on maintaining habitat heterogeneity within forested landscapes.

Mechanisms of community change

Within this system, community response to disturbance appeared to be primarily driven by colonization dynamics. In both disturbance scenarios, exotic species invasion and drought, colonization rates changed and led to altered community composition with disturbance. Exotic species invasion impacts were driven by establishment limitation occurring within invaded sites. As the community recovered from drought species re-colonization and invasion led to altered community composition. Although extinction occurred within the context of both disturbances it was not found to be a factor driving community changes with perturbation in the system.

Although the mechanisms of community change were uniform across disturbance type, changes occurred at a local scale and not across the entire community with disturbance. In general, disturbance resulted in more stochastic site and species responses than large-scale shifts in community composition. Invasion impacts are inherently spatially restricted, such that impacts were only observed in those areas where invasion occurred. In both scenarios, field was consistently important in determining both invasion and drought impacts. At the species level I found wide variation in invasion and drought impacts on individual species. Impacts varied across the site most likely as a result of differing disturbance histories and species trajectories within each of the study fields. While local disturbance impacts appeared to depend on the local propagule pool, competitive stress and resource availability rather than on coarse scale site characteristics.

Within this study, the species turnover conceptual framework was applied to community dynamics to elucidate common mechanisms of community change. The study resulted in several interesting findings that improved our understanding of the mechanisms governing community response to disturbance and allowed us to make testable predictions on the response of communities to perturbation. This approach can be used in other systems to determine the generality of these mechanisms as drivers of community change across a suite of disturbance types.

LITERATURE CITED

Allen, C.D. & Breshears, D.D. (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences*, **95**, 14839-14842.

Anderson, R.C., Loucks, O.L. & Swain, A.M. (1968) Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. *Ecology*, **50**, 255-263.

Bard, G.E. (1952) Secondary succession on the piedmont of New Jersey. *Ecological Monographs*, **22**, 195-215.

Bartha, S., Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2003) Plant colonization windows in a mesic old field succession. *Applied Vegetation Science*, **6**, 205-212.

Bazzaz, F.A. (1996) *Plants in Changing Environments*. Cambridge University Press, Cambridge.

Beatty, S.W. (2003) Habitat heterogeneity and maintenance of species in understory communities. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp 177-197, Oxford University Press, Oxford.

Bever, J.D. (2003) Soil community feedback and the coexistance of competitors: conceptual frameworks and empirical tests. *New Phytologist*, **157**, 465-473.

Blomqvist, M.M., Vos, P., Klinkhamer, P.G.L. & ter Keurs, W.J. (2003) Declining plant species richness of grassland ditch banks- a problem of colonization or extinction. *Biological Conservation*, **109**, 391-406.

Blossey, B. (1999) Before, during and after: the need for long-term monitoring in invasive species management. *Biological Invasions*, **1**, 301-311

Bollinger, E.K., Harper, S.J. & Barrett, G.W. (1990) Effects of seasonal drought on old-field plant communities. *American Midland Naturalist*, **125**, 114-125.

Bosy, J.L. & Reader, R.J. (1995) Mechanisms under the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. *Functional Ecology*, **9**, 635-639.

Brandon, A.L., Gibson, D.J. & Middleton, B.A. (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biological Invasions*, **6**, 483-493.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445-449.

Brown, R.L. & Fridley, J.D. (2003) Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. *Okios*, **102**, 15-24.

Buell, M.F., Buell, H.F., Small, J.A. & Monk, C.D. (1961) Drought effect on radial growth of trees in the William L. Hutcheson Memorial Forest. *Bulletin of the Torrey Botanical Club*, **88**, 176-180.

Buell, M.F., Buell, H.F., Small, J.A. & Siccama, T.G. (1971) Invasion of trees and secondary succession on the New Jersey Piedmont. *Bulletin of the Torrey Botanical Club*, **98**, 67-74.

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

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D.

(2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630-640.

Cahill, J.F. (2003) Neighbourhood-scale diversity, composition and root crowding do not alter competition during drought in a native grassland. *Ecology Letters*, **6**, 599-603.

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521-523.

Callaway, R.M., Ridenour, W.M., Laboski, T., Weir, T. & Vivanco, J.M. (In press) Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology*.

Casper, B.B., Schenk, H.J. & Jackson, R.B. (2003) Defining a plant's belowground zone of influence. *Ecology*, **84**, 2313-2321.

Christian, J.M. & Wilson, S.D. (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology*, **80**, 2397-2407.

Cleland, E.E., Smith, M.D., Andelman, S.J., Bowles, C., Carney, K.M., Horner-Devine, M.C., Drake, J.M., Emery, S.M., Gramling, J.M. & Vandermast, D.B. (2004) Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters*, **7**, 947-957.

Cole, P.G. & Weltzin, J.F. (2005) Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. *Biological Invasions*, **7**, 477-488.

Condit, R. (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change*, **39**, 413-427.

Condit, R., Hubbell, S.P. & Foster, R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419-439.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **193**, 1302-1310.

Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171-207.

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

Dalling, J.W., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, **86**, 674-698.

D'Antonio, C.M., Flint, H.R., Mack, M., Hitchcock, D. & Vitousek, P.M. (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *Journal of Vegetation Science*, **9**, 699-712.

Davis, M.A., Grime, P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528-534

Davis, M.A. & Pelsor, M. (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters*, **4**, 421-428.

Davison, S.E. & Forman, R.T.T. (1982) Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bulletin of the Torrey Botanical Club*, **109**, 64-73.

Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, **95**, 565-574.

Delissio, L.J. & Primack, R.B. (2003) The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology*, **19**, 489-500.

Duffy, D.C. & Meier, A.J. (1992) Do Appalachian herbaceous understories ever recover from clearcutting? Conservation Biology, 6, 196-201.

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

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: Light interception and effects on an old-field plant community. *Ecology*, **73**, 1024-1031.

Fargione, J., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Science*, **100**, 8916-8920.

Fenner, M. (1987) Seedlings. *New Phytologist*, **106**, 35-47.

Fox, B.J. (1987) Species assembly and the evolution of community structure. *Evolutionary Ecology*, **1**, 201-213.

Gleason, H.A. & Cronquist, A. (1991) *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. New York Botanical Garden, Bronx.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd edn. John Wiley & Sons, Chichester.

Grime, J.P., Willis, A.J., Hunt, R. & Dunnett, N.P. (1994) Climate-vegetation relationships in the Bibury road verge experiments. *Long-term Experiments in Agricultural and Ecological Sciences* (eds R.A. Leigh & A.E. Johnston), pp. 271-285, CAB International, Wallingford.

Grubb, P.J. (1988) The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. *Annales Zoologici Fennici*, **25**, 23-36.

Hager, H.A. (2004) Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia*, **139**, 140-149.

Hager, H.A. & McCoy, K.D. (1998) The implications of accepting untested hypotheses: a review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation*, **7**, 1069-1079.

Hanson, P.J. & Weltzin, J.F. (2000) Drought disturbance from climate change: response of United States forests. *The Science of the Total Environment*, **262**, 205-220.

Husband, B.C & Barrett, S.C.H. (1996) A metapopulation perspective in plant population biology. *Journal of Ecology*, **84**, 461-469.

Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M. & Zinnel, K.C. (1987) Old-field succession on a Minnesota sand plain. *Ecology*, **68**, 12-26.

Jongejans, E. & de Kroon, H. (In press) Space versus time variation in the population dynamics of three co-occuring perennial herbs. *Journal of Ecology*.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & McCarron, J.K. (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, **298**, 2202-2205.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Goth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286-293.

Kobe, R.K. & Coates, K.D. (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Colombia. *Canadian Journal of Forest Research*, 27, 227-236.

Larsen, C.P.S. & MacDonald, G.M. (1998) Fire and vegetation dynamics in a jack pine and black spruce forest reconstructed using fossil pollen and charcoal. *Journal of Ecology*, **86**, 815-828.

Laurance, W.F., Williamson, G.B., Delamônica, P., Oliveira, A., Lovejoy, T.E., Gascon, C. & Pohl, L. (2001) Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology*, **17**, 771-785.

Leitner, L.A., Dunn, C.P., Guntenspergen, G.R., Sterns, F. & Sharpe, D.M. (1991) Effects of site, landscape features, and fire regime on vegetation patterns in presettlement southern Wisconsin. *Landscape Ecology*, **5**, 203-217.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B*, **270**, 775-781.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237-240.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Mack, M.C. (2003) Phylogenetic constraint, absent life forms, and preadapted alien plants: a prescription for biological invasions. *International Journal of Plant Sciences*, **164** (suppl.), S185-S196.

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

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography*, **24**, 633-644.

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

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2004) Beyond biodiversity: individualistic controls of invasion in a self-assembled community. *Ecology Letters*, **7**, 121-126.

Morecroft, M.D., Masters, G.J., Brown, V.K., Clarke, I.P., Taylor, M.E. & Whitehouse, A.T. (2004) Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Functional Ecology*, **18**, 648-655.

Myster, R.W. & Pickett, S.T.A. (1990) Initial conditions, history and successional pathways in ten contrasting old fields. *American Midland Naturalist*, **124**, 231-238.

Myster, R.W. & Pickett, S.T.A. (1994) A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology*, **75**, 387-392.

O'Neill, E.G., Johnson, D.W., Ledford, J. & Todd, D.E. (2003) Acute seasonal drought does not permanently alter mass loss and nitrogen dynamics during decomposition of red maple (Acer rubrum L.) litter. *Global Change Biology*, 9, 117-123.

Osmond, C.B., Austin, M.P., Berry, J.A., Billings, W.D., Boyer, J.S., Dacey, J.W.H., Nobel, P.S., Smith, S.D. & Winner, W.E. (1987) Stress physiology and the distribution of plants. *BioScience*, **37**, 38-48.

Ouborg, N.J. (1993) Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. *Oikos*, **66**, 298-308.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3-19.

Pickett, S.T.A. (1982) Population patterns through twenty years of oldfield succession. *Vegetatio*, **49**, 45-59.

Pickett, S.T.A. & Cadenasso, M.L. (2005) Vegetation dynamics. Vegetation Ecology, (ed E. van der Maarel), pp 172-198, Blackwell Publishing, Malden.

Prieur-Richard, A.H., Lavorel, S., Grigulis, K. & Dos Santos, A. (2000) Plant community diversity and invasibility by exotics: invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. *Ecology Letters*, **3**, 412-422.

Rejmánek, M. (1989) Invasibility of plant communities. *Biological Invasions: a Global Perspective* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 369-388. John Wiley & Sons, Chichester.

Rejmánek, M. & Rosén, E. (1992) Influence of colonizing shrubs on species-area relationships in alvar plant communities. *Journal of Vegetation Science*, **3**, 625-630.

Roberts, M.R. & Gilliam, F.S. (2003) Response of the herbaceous layer to disturbance in Eastern forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp 302-320, Oxford University Press, Oxford.

Scheffer, M., Carpenter, S., Foley, J.A., Folkes, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591-596.

Schoener, T.W. (1983) Field Experiments on interspecific competition. *American Naturalist*, **122**, 240-285.

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

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Stampfli, A. & Zeiter, M. (2004) Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. *Journal of Ecology*, **92**, 568-576.

Sternberg, M., Brown, V.K., Masters, G.J. & Clarke, I.P. (1999) Plant community dynamics in a calcareous grassland under climate change manipulation. *Plant Ecology*, **143**, 29-37.

Stevens, M.H.H., Bunker, D.E., Schnitzer, S.A. & Carson, W.P. (2004). Establishment limitation reduces species recruitment and species richness as soil resources rise. *Journal of Ecology*, **92**, 339-347.

Symstad, A.J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology*, **81**, 99-109.

Tilman, D. (1985) The resource ratio hypothesis of plant succession. *American Naturalist*, **125**, 827-852.

Tilman, D. (1993) Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, **74**, 2179-2191.

Tilman, D. (1997) Mechanisms of Plant Competition. *Plant Ecology* 2nd ed. (ed M. J. Crawley), pp. 239-261. Blackwell Science, Oxford.

Tilman, D. & El Haddi, A. (1992) Drought and biodiversity in Grasslands. *Oecologia*, **98**, 257-264.

Turner, M.G., Romme, W.H. & Tinker, D.B. (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **7**, 351-358.

Ugolini, F.C. 1964 Soil development on the red beds of New Jersey. *William L. Hutcheson Memorial Forest Bulletin*, **2**, 1-34.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller, D. & Matson, P.A. (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, **238**, 802-804.

Von Holle, B., Delcourt, H.R. & Simberloff, D. (2003) The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science*, **14**, 425-432.

Von Holle, B. & Simberloff, D. (2004) Testing Fox's assembly rule: does plant invasion depend on recipient community structure? *Oikos*, **105**, 551-563.

Walker, S., Wilson, J.B. & Lee, W.G. (2005) Does fluctuating resource availability increase invisibility? Evidence from field experiments in New Zealand short tussock grassland. *Biological Invasions*, **7**, 195-211.

Williamson, M. (1996) *Biological Invasions*. Chapman and Hall, London.

Yurkonis, K.A. & Meiners, S.J. (2004) Invasion impacts local species turnover in a successional system. *Ecology Letters*, **7**, 764-769.