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Invasion as an opportunity to study community assembly in response to competition, recovery from drought, phenology

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Invasion as an opportunity to study community assembly in response to competition, recovery from drought, phenology

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in

Biology

by

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The Dissertation of Chandler E. Puritty is approved and is acceptable in quality and form for publication on microfilm and electronically:

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DEDICATION

I dedicate this dissertation to all my soul family through space and time. This is just the beginning.

EPIGRAPH

We feel the beauty of nature because we are part of nature and because we know that however much in our separate domains we abstract from the unity of Nature, this unity remains. Although we may deal with particulars, we return finally to the whole pattern woven out of these.

Ernest Everett Just

But I feel like I have enough knowledge to get me by in life. Obviously, I dont know everything, but I feel like I have enough knowledge to get me through.

Kodak Black

While loss of habitat and species, pollution, and what we typically think of as environmental problems remain important issues for me, after walking across America listening and studying the environment for 17 years, I realize that people are part of the environment

John Francis

I don’t really know why I care so much. I just have something inside me that tells me that there is a problem, and I have got to do something about it. I think that is what I would call the God in me

Wangari Maathai

TABLE OF CONTENTS

Signature Page iii

Dedication iv

Epigraph v

Table of Contents vi

List of Figures viii

List of Tables x

Acknowledgements xii

Vita xiii

Abstract of the Dissertation xiv

Introduction 1

Chapter 1 Different traits predict competitive effect versus response by *Bromus madritensis* in its native and invaded ranges 13

Chapter 2 Drought in Southern California coastal sage scrub reduces herbaceous biomass of exotic species more than native species, but exotic growth recovers quickly when drought ends 28

Chapter 3 Legacy of severe drought shifts ecosystem towards later phenology during recovery 49
- 3.1 Abstract 50
- 3.2 Introduction 50
- 3.3 Methods 54
  - 3.3.1 Species Level Phenology 56
  - 3.3.2 Predictive Power of Phenology Traits 56
  - 3.3.3 Traits 57
  - 3.3.4 Ecosystem Level Phenology 57
  - 3.3.5 Statistical Analysis 57
- 3.4 Results 59
  - 3.4.1 Species Level Phenology 59
  - 3.4.2 Predictive Power of Phenology Traits 59
  - 3.4.3 Ecosystem Level Phenology 60
- 3.5 Discussion 60
  - 3.5.1 Species Level Phenology 62
  - 3.5.2 Predictive Power of Phenology Traits 63

3.5.3 Ecosystem Level Phenology 64
3.6 Conclusion 65

Conclusion 82

LIST OF FIGURES

Figure 1.1. Above-ground biomass of *B. madritensis* individuals (in grams) from seeds collected in the native range (Spain) and invaded range (California), grown with and without interspecific competition 19

Figure 1.2. **a** Competitive effect of *B. madritensis* originating from each population. **b** Average value of *B. madritensis* competitive effect on all resident species in each place of origin. 20

Figure 1.3. **a** Competitive response of *B. madritensis* originating from each population. **b** Average value of *B. madritensis* competitive response to all resident species tested from each place of origin. 21

Figure 2.1. Growing season precipitation (October–April) at the experimental site over the last 30years 33

Figure 2.2. Conceptual figure of the experimental design 34

Figure 2.3. Herbaceous biomass versus total growing season rainfall during the experimental drought (2013–2016, **a, b**) and recovery (2017, **c, d**) stages 37

Figure 2.4. Number of germinating individuals from soils collected in October 2016, following 4 years of experimental drought treatments 39

Figure 2.5. Species percent cover in response to precipitation amount during the experimental drought (2013–2016, **a, b**) and recovery year (2017, **c, d**) 41

Figure 3.1. NDVI on each measurement date for each of the 10 species grown in monocultures in a single season 71

Figure 3.2. Mean abundance of *C. melitensis* as shown by percent cover in the field at SMER across all drought treatments and over two years (2016 drought, 2017 recovery) 72

Figure 3.3. Community weighted flowering phenology trait means for (a) end, (b) duration, (c) start, and (d) peak across all drought treatments over two years (2016 drought, 2017 recovery) 73

Figure 3.4. Unweighted bloom duration trait means for native (green) and exotic (gold) species. Color corresponds to origin 74

Figure 3.5. Community bloom duration means weighted separately for exotic and native communities on severe drought and ambient precipitation plots during the recovery year (2017) 75

Figure 3.6. NDVI on each measurement date for open plots dominated by herbaceous species, and shrub cover plots, during drought (2016) and recovery (2017) 76

Figure 3.7. NDVI peak date plotted against community weighted bloom duration means 77

LIST OF TABLES

Table 1.1. Resident species and target species utilized in the experiment, including the abbreviation used in figures, common name, functional group and mean functional traits 17

Table 1.2. Functional trait differences between *B. madritensis* (BRMA) collected in California (CA) versus Spain (ES) and between the suites of resident species chosen from California versus Spain 20

Table 1.3. Effects of origin and resident species identity (nested within origin) on competitive response and competitive effect of *B. madritensis* 21

Table 1.4. The relative importance of resident functional traits for predicting the competitive effect of *B. madritensis* on resident species from Spain or California 22

Table 1.5. The relative importance of resident species functional traits for predicting the competitive response of *B. madritensis* to being grown with each resident species from Spain or California 22

Table 2.1. Summary of community composition averaged across all experimental plots during the 5-year experiment, including species origin, life history , mean total cover, fraction of total cover, species richness, and mean total herbaceous biomass 36

Table 2.2. Statistics from linear models evaluating how species origin (native/exotic) and rainfall influenced herbaceous biomass during four years of experimental rainfall manipulation (response during 2013–2016 growing seasons), and in the recovery year (2017 growing season) 36

Table 2.3. Biomass responses to drought treatments (2012–2016) as influenced by both concurrent and antecedent factors 38

Table 2.4. Statistics from linear models evaluating how native versus exotic origin (Origin) and experimental drought treatments (Treatment) influenced variance in the abundance of germinating seeds from the seedbank, for soils collected in October 2016, following four growing seasons 39

Table 2.5. Recovery following drought (2017) as influenced by both concurrent and antecedent factors 40

Table 2.6. Statistics from linear models evaluating how species life history (annual/perennial) and rainfall influenced percent cover during 4 years of experimental rainfall manipulation (response during 2013–2016 growing seasons), and in the recovery year (2017 growing season) 40

Table 3.1. Target species from SMER utilized in the experiment, including origin, life history, flowering phenology traits and growth habit 67

Table 3.2. Summary of the effect of drought treatment and year (2016 drought, 2017 recovery) on *C. melitensis* field abundances at SMER 68

Table 3.3. Summary of the effect of year and treatment on community weighted flowering phenology trait means (duration, peak, begin, end) at SMER experiment on all treatments and both years (2016 drought, 2017 recovery) 68

Table 3.4. Summary of the effect of year on community weighted flowering phenology duration means across all treatments 69

Table 3.5. Summary of the effect of treatment on community weighted bloom duration for native compared to exotic species 69

Table 3.6. Summary of the effect of community composition (shrub cover or open herbaceous) and drought treatments on productivity as measured by NDVI for each time point in a single growing season (2017 recovery) 70

Table 3.7. Summary of the effect of treatment, community weighted bloom duration means, and any interactions on plot level date at peak NDVI at SMER in the recovery year 71

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Chapter 1, in full, is a reprint of the material as it appears in: Puritty CE, Mayfield MM, Azcrate FM, Cleland EE (2018) Different traits predict competitive effect versus response by *Bromus madritensis* in its native and invaded ranges. Biological Invasions:1-13. The dissertation author was the primary investigator and author of this paper.

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Chapter 3, in part is currently being prepared for submission for publication of the material. Puritty, Chandler E.; Esch, Ellen H.; Cleland, Elsa E.; Lipson, David A.; The dissertation author was the primary investigator and author of this material.

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ABSTRACT OF THE DISSERTATION

Invasion as an opportunity to study community assembly in response to competition, recovery from drought, phenology

by

Chandler E. Puritty

Doctor of Philosophy in Biology

University of California San Diego, 2019

Professor Elsa Cleland, Chair

Species interactions in invaded ecosystems are important to understand for predicting future changes in the system and are particularly crucial in the context of global climate change and increasing climate variability. Southern Californias predominately shrub dominated ecosystems are being invaded by exotic annual species and are predicted to experience increasingly severe drought. It remains unclear how these shifts in species composition combined with inter-annual climate variability may leave a legacy that affects ecosystem functioning beyond the duration of the disturbance. In this dissertation, I tested the hypothesis that invasion can alter ecosystem function and recovery from drought. Chapter 1 shows that traits rather than fitness differences are

most important when predicting competitive outcomes between native and exotic focal species. I found that different combinations of traits may aid in determining which species are most likely to strongly compete with invaders versus those that will be competitively suppressed by invaders. This demonstrates the complexity of the interactions between the native and exotic species in their immediate interactions. Chapter 2 scales up to see how these competitive interactions play out at the ecosystem level in a natural system. I found that native biomass was more resistant to changes in response to drought but that exotic biomass was more resilient in returning to pre-drought abundances in its recovery from drought. The greater decline in exotic biomass with drought was likely driven by life-history differences between native and exotic species in this system, where exotic species are more likely to have an annual life history, and native species are more likely to be perennial. This chapter demonstrated that when exotic and native species differ in life history they may also vary in their resistance and resiliency in response to climate extremes such as drought. Chapter 3 documents how the shifting species composition observed in chapter 2 influenced ecosystem functioning during recovery from drought, particularly with regard to phenology. I found that the most severe drought plots exhibited higher abundances of species with longer blooming phenology duration and ecosystem level shift towards later phenology. I showed that drought can leave a multi-year legacy on these communities that continues once the disturbance has ended. In sum this dissertation shows that invasion alters ecosystem recovery from severe drought as measured by productivity, biomass, and ecosystem level phenology and indicates the importance of evaluating the impact of a disturbance even once recovery has begun.

Introduction

Semi-arid and arid systems occupy 40 percent of terrestrial land (Reynolds et al. 2007). These systems include Mediterranean climates that are characterized by wet cool winters and hot dry summers (Axelrod 1973). Soil water is a crucial limiting resource for growth in Mediterranean-type shrub lands (Mooney 1981). The outstanding inter-annual variability in precipitation in Mediterranean climates has been projected to increase in response to global climate change with both wet and dry events predicted to increase in number and severity (Cubasch et al. 2001; Durack et al. 2012). Environmental variability plays a central role in determining the structure and function of many biological communities (Elmendorf and Harrison 2009; Hobbs et al. 2007) Furthermore, many Mediterranean systems including California have been invaded by European exotic annual grasses (D'Antonio and Vitousek 1992).The native shrub species in Mediterranean systems are functionally quite distinct from the exotic annual grasses and its likely that they will respond differently to the changing climate (Hobbs and Mooney 1995). Studying an on-going invasion presents a novel opportunity to learn about community composition and assembly in real-time. It is increasingly important to understand how these systems will respond to the projected precipitation extremes particularly in terms of species interactions, competition and ecosystem functioning during and between these extreme precipitation gradients.

Invasions by alien plant species threaten native ecosystems by reducing local plant species diversity and increasing plant production of the invaded community (Mack et al. 2000; Vil et al. 2011). Increased plant production and subsequent resource availability enables population growth for alien species and provides other invading species with an opportunity to colonize

(Hood and Naiman 2000). When this is combined with high levels of disturbance, such as drought, an introduced species can become invasive (Huston 2004). Additionally, the predicted increase in intense rain events will create the opportunity for invasion but the long term effect on community dynamics is largely unknown. Understanding the mechanisms driving these widespread invasions is essential to the restoration of native ecosystems and for predicting the effects of global climate change on invaded systems (Dukes and Mooney 1999).

Interspecific competition is considered one of the most important processes in predicting the likelihood of plant invasion success (Crawley and Ross 1990; MacArthur 1970) and a meaningful way to quantify plant-plant interactions. An understanding of the role of competition in plant invasions requires the study of both the ability of the invader to grow and increase in population size in the recipient community, and the recipient communitys tolerance of the invading species (Levine et al. 2003). The combination of biotic and abiotic factors that promote invasion may be predictable on the basis of community ecology theories regarding community assembly and species coexistence in diverse plant communities (Shea and Chesson 2002).

Pattison et al. (1998) first hypothesized that successful invaders have morphological and physiological traits which increase light capture, utilization efficiency, and ultimately, plant fitness. Later studies support this, showing that invasive species are often characterized by traits related to rapid growth and widespread dispersal (Van Kleunen et al. 2010). Invasive species are likely to be those among the introduced species that have a suite of traits that grants them the highest competitive ability (Vila and Weiner 2004). The empty niche hypothesis states that the recipient community is unsaturated by native species so invaders with distinct functional traits can use the spare resources and occupy the unused niches (Hierro et al. 2005; MacArthur 1970). The limiting similarity hypothesis predicts that successful invaders are functionally distinct from species in the recipient community and thus encounter less competition and can fill an empty niche (Callaway and Ridenour 2004; Hierro et al. 2005; MacArthur and Levins 1967; Mack 2003; Vitousek et al. 1987). Instead of saying that a certain set of functional traits cause invasion, this hypothesis takes into consideration the difference in traits between the recipient and invading communities which may differ by ecosystem type. An alternative hypothesis suggests that any trait-based differences between species are likely less important for predicting competitive hierarchies than are simple fitness differences which are based solely on the relative differences in size of individuals (Godoy et al. 2014). Thus, monitoring species traits and competitive outcomes during the progression of natural invasions allows ecologists to test these community assembly theories in real time and project the direction of species and community level responses to extreme events.

Ecosystem response to drought disturbance can be quantified by how sensitive the system is to disturbance or resistance (D'antonio and Thomsen 2004) and by its ability to recover following a disturbance or resilience (Gunderson 2000) Resistance and resilience can be conferred through biodiversity, productivity, ecosystem functioning, phenology etc. (Holling 1973; Lavorel 1999; Naeem et al. 2000; Peterson et al. 1998). This framework accounts for the understanding the ways in which the consequences of a disturbance could last well beyond the duration of a drought and is particularly useful for evaluating how species with distinct life histories might differ in their response to disturbance (Hoover et al. 2014; Miller and Chesson 2009).

Predictions regarding responses to impending environmental changes are often based on standing community assembly with the assumption that the most abundant species will be the species whose response most influences ecosystem functioning (Lavorel and Garnier 2002). Standing community assembly is difficult to quantify in a system undergoing invasion (Dukes 2002). As climate conditions continue to shift, we expect that the community composition of these ecosystems will reflect the changes in the resource pool (Cleland et al. 2013).

Community composition and biodiversity in particular play an important role in the way ecological systems respond to environmental changes (Chapin et al. 1997; Steffen et al. 1996) in light of their effects on long term stability of ecosystem productivity and function (Tilman 1996). Suding et al. (2008) argues that community-level changes, can increase or decrease the physiological responses causing changes in ecosystem functioning that cannot be predicted by individual responses. For example, species turnover in a community could help or hinder a communitys ability to respond to global change. Different ecosystems offer different resources and climate change has the potential to shift the environmental conditions of native communities and leave them more susceptible to invasion and shifts in ecosystem functioning (Lyons and Schwartz 2001). Shifts in the proportion of grasses versus shrubs in a semi-arid system would likely manifest as changes in the structure and function of the ecosystem (Brown et al. 1997; Jackson et al. 2002; Schlesinger et al. 1990). It is unclear how long these changes in ecosystem and structure could persist following a disturbance.

In this context, ours is an interesting system for addressing these questions. Southern California is home to one of the most dramatic ecological invasions worldwide: the replacement of native perennial grasses by exotic annual grasses and forbs across 9.2 million hectares of grasslands (D'Antonio and Vitousek 1992). As a result, much of the native coastal sage scrub community has been lost (Klopatek et al. 1979; Westman 1987). What remains of coastal sage scrub is highly fragmented and is experiencing an accompanying decline in faunal (Soul et al. 1992; Soul et al. 1988) and floral (Alberts et al. 1993) diversity.

Mediterranean-type ecosystems like coastal sage scrub tend to have a high intrinsic resistance to drought (Penuelas et al. 2001) and resilience to disturbances such as fire (Bond and van Wilgen 1996; Keeley 1986). This resilience in largely due to ecological diversity, especially functional diversity in the form of the coexistence of a variety of plant life histories (Keeley 1986; Malanson and Trabaud 1987; Trrega et al. 1995). Studies often find that drought-induced structural changes in the vegetation reduced ecosystem level production in the subsequent year (Reichmann et al. 2013; Sala et al. 2012; Yahdjian and Sala 2006). Unfortunately, sites with greater numbers of rare species, like coastal sage scrub, are most likely to see richness and diversity decline in response to inter-annual climate variability (Alberts et al. 1993; Oksanen 1996). The slow-growth rates and allocation to often woody like structures makes them much more resilient to environmental stressors as compared to seedlings or short-lived annuals (Kelly and Bowler 2002).

Unlike Californias majority perennial species, these introduced annual species have traits associated with high resource acquisition (Garnier 1992). These annual grasses have shallow, fibrous root systems which help them take advantage of sporadic rain events (Ellern et al. 1970; Gordon and Rice 1993). They germinate soon after the first rains of the season (Mahall et al. 1981) and maintain high transpiration and growth rates throughout the wet season thus depleting soil water (Davis and Mooney 1985; Ewing and Menke 1983). Once the dry season begins, these annual grasses produce many seeds and die; their offspring waiting for the next wet season (Heady 1956). As a result, under chronic disturbance, annual grasslands tend to persist (Callaway and Davis 1993; Freudenberger et al. 1987).

Hoover et al (2014) found that an extreme reduction in ecosystem function that could be attributed to drought did not prevent rapid ecosystem recovery in a grassland ecosystem. However, this apparent resilience was limited to productivity as the community composition did not revert back (Hoover et al. 2014). Studies in semi-arid systems highlight the importance of antecedent conditions, or lag effects, for predicting plant growth (Potts et al. 2006), but the influence of lagged drought effects on ecosystem functioning in an invaded system remains largely unexplored.

Understanding the mechanisms surrounding the success of these grasses is particularly important in the context of a rapidly changing climate. Soil water is a crucial limiting resource for growth in Mediterranean-type shrub lands (Mooney 1981). Climate change, which can take the form of prolonged droughts and excessively wet years, changes the environmental conditions of native communities and leaves them susceptible to invasion via niche opportunities. As a Mediterranean system, Southern California chaparral experiences high inter-annual variability in rainfall and thus it remains crucial to understand how the community responds not only to drought but also to the wet years in between with an understanding that the effects of drought have the potential to persist.

This thesis focuses on the mechanisms underlying the long term invasion of exotic large European annual grasses into coastal sage scrub and how varying precipitation effects the community composition and ecosystem functioning of the system during recovery from drought. The dissertation consists of three chapters examining this invasion from a multi-scale perspective ranging from species level response to competition to community level and ecosystem functioning responses to precipitation variation. In chapter 1, I used species functional traits and competitive outcomes to evaluate the role of competition in the invasion success of a dominant European annual grass. Chapter 2 explored how invasion effects the resistance and resilience of native and exotic biomass during and recovering from drought. Chapter 3 focused on the long term effects of invasion and drought on ecosystem functioning and recovery.

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Chapter 1

Different traits predict competitive effect versus response by *Bromus madritensis* in its native and invaded ranges

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ORIGINAL PAPER

Different traits predict competitive effect versus response by *Bromus madritensis* in its native and invaded ranges

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Abstract Community assembly and coexistence theories predict that both fitness and plant functional traits should influence competitive interactions between native and invasive species. The evolution of the increased competitive ability hypothesis predicts that species will grow larger (a measure of fitness) in their invaded than native range; hence we hypothesized that species might exert greater competitive effects in their invaded range, lessening the importance of functional traits for competitive outcomes. In a greenhouse experiment we compared traits and competitive interactions between *Bromus madritensis* (an annual grass) and resident species from its native range in Spain, and its invaded range in Southern California. As predicted, *B. madritensis* collected in California grew larger and had a greater competitive effect on resident species than *B. madritensis* collected in Spain. However, residents from California also suppressed the growth of *B. madritensis* more than species from its native range in Spain. Competitive interaction strengths were predicted by different suites of traits in the native versus invaded range of *B. madritensis*; surprisingly, however, size of the resident species (fitness), did not predict variation in competitive interactions. This study shows that different suites of traits may aid in identifying those native species likely to strongly compete with invaders, versus those that will be competitively suppressed by invaders, with important implications for the design of restoration efforts aimed at promoting native species growth and preventing invasion. More generally, our study shows that fitness differences may not be as important as traits when predicting competitive outcomes in this system.

Keywords Coexistence · EICA · Fitness differences · Functional traits · Limiting similarity

Introduction

Invasive plants impact ecosystem processes (Liao et al. 2008) and biodiversity, reducing the richness and abundance of native species at local scales (Powell et al. 2011; Vilà et al. 2011). Although the

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mechanisms that underlie these impacts are increasingly understood (Levine et al. 2003), there is great variation among invader species in how they impact resident communities, with some exotic species having strong effects, and others having little or no impact (Pyšek et al. 2012). Theory in invasion biology often relies on plant functional traits to reflect species' ecological strategies, and indeed invasive species often possess traits that differ from non-invasive or native species (Pyšek and Richardson 2008; Van Kleunen et al. 2010). While there has been a call to evaluate whether traits related to the likelihood of invasion correspond to the impacts of invasive species (MacDougall et al. 2009; Pyšek et al. 2012), few empirical studies on the topic exist.

Theories from community ecology predict that functional traits and measures of plant fitness should influence both the likelihood that a species will invade, and the competitive impact of the invader on resident species. For instance, the theory of limiting similarity posits that species with overlapping niches will compete strongly for resources, such that successful invaders must be functionally dissimilar from residents to succeed (Abrams 1983; MacArthur and Levins 1967; Schwilk and Ackerly 2005). Consistent with this theory, plant functional traits often reflect variation in strategies of life-history and resource-capture (Diaz et al. 1998; Lavorel and Garnier 2002), and experimental tests often find that invaders with traits similar to residents have a lower probability of invading than those with traits that differ from residents (Dukes 2002; Emery 2007; Fargione et al. 2003; Von Holle and Simberloff 2004). A recent meta-analysis suggests that while many studies show support for a role of limiting similarity in predicting the likelihood of invader establishment, the performance of established invasive species is not influenced by the traits of resident species (Price and Pärtel 2013).

Coexistence theory predicts that a species can invade a new system in the absence of niche differences if fitness differences favor the invading species over the resident species (Chesson 2000; MacDougall et al. 2009). Invasive species are often larger or have higher seed set than non-invasive species from their home ranges (Jelbert et al. 2015), suggesting a general competitive advantage for invader species. Invaders also often achieve larger sizes in their invaded ranges than in their home ranges, a pattern that is also suggestive that these species have a general fitness advantage (Crawley 1987; Parker et al. 2013).

The evolution of increased competitive ability hypothesis (EICA) predicts that selection will act upon invading species that have escaped their specialist enemies (Keane and Crawley 2002), resulting in reduced allocation to defense and increased allocation to vegetative growth (Blossey and Notzold 1995). Few studies have explicitly evaluated the relative roles of trait and fitness differences to predict the outcome of competitive interactions between native and invading species. A recent study demonstrated that while some species invade by competitively excluding residents, other invaders may be successful by having traits and relative fitness differences that enable coexistence with resident species (Lai et al. 2015).

Traits may be differentially important for understanding the competitive effect of invaders on residents versus the competitive response of invaders to the resident community (sensu Goldberg 1990). Traits related to plant size (a proxy for fitness), for instance, are thought to relate to the ability to draw down many resources simultaneously, potentially explaining the concordance between competitive hierarchies based on competitive effect versus response (Goldberg and Landa 1991). Leaf trait values, such as high specific leaf area (SLA) that correlate with rapid growth plant life strategies (Wilson et al. 1999) and high rates of resource capture (Garnier et al. 2001) have been associated with invader success (Feng et al. 2008; Grotkopp and Rejmánek 2007), while traits associated with high resource-use efficiency predict which systems might be invaded (Funk and Vitousek 2007). Fast germination is another trait that has been hypothesized to confer a seasonal priority-advantage to early-active species, and has been found to be associated with non-native species that can competitively suppress later-germinating native species (Wainwright et al. 2012).

Trait-based competitive hierarchies have been described in many systems, from forests to annual-dominated communities (Kraft et al. 2014; Kunstler et al. 2012), but few have focused on the competitive interactions of species in their native and invaded ranges (García et al. 2013). A key study found that competition from neighbors caused a greater reduction in the growth of *Centaurea strobe* in its native than invaded range, although the mechanism was not identified (Callaway et al. 2011). If evolved competitive ability contributes to invasion success, and invasion releases exotic species from stabilizing controls like herbivores and diseases, then invading species should exhibit differences in traits between the invaded and native range. Therefore, the relative roles of trait differences versus competition-based fitness differences for predicting competition outcomes may vary between a species in its native and invaded ranges.

In this study, we aimed to determine the relative roles of functional traits and fitness differences for predicting the response of an invader to competition with residents and the competitive effect of the invader on residents. To do this, we focused on the invasive species *Bromus madritensis* (common name: compact brome), an annual grass, native to western and southern Europe. *B. madritensis* has become a problematic invader in Southern California and in other Mediterranean systems (e.g. Wainwright et al. 2016) within the last 300 years (Watson 1880). We focus on two populations of *B. madritensis*—one from within its native range (Madrid, Spain—'native') and one from within its invaded range (Southern California—'invaded'), and evaluated its competitive interactions with resident species from each region. We hypothesized that:

1. *B. madritensis* would achieve larger size (a proxy for fitness, Younginger et al. 2017) and have different trait means in its invaded than native range, consistent with the EICA hypothesis, and that as a result,
2. *B. madritensis* would have a lower competitive response to residents in the invaded community than residents in its native community,
3. *B. madritensis* would have a greater competitive effect on residents in the invaded community than residents in its native community, and
4. competitive outcomes would be driven by a combination of fitness and trait differences, but that fitness differences would play a greater role in invader success in the invaded range.

Methods

Seed collection

Resident species for this experiment are listed in Table 1. Seed collections were collected from one site each in Spain and California, meaning that the experiment compares just two populations of the focal species. In Spain, seeds of *B. madritensis* and the most commonly co-occurring species were collected by Francisco Martín Azcárate in the Spring of 2014, near the municipality of Colmenar Viejo, 30 km north of Madrid (approx. 850 m altitude). The site has a granite substrate, and a typical mediterranean climate (13.5 °C mean annual temperature, 550 mm mean annual rainfall, severe summer drought). Seeds were collected from as many plants as possible, keeping a distance of at least 10 m between individuals.

In California, seeds of *B. madritensis* and common, co-occurring species were collected from the UC San Diego Ecological Park in May 2015. This time period corresponded with an extreme drought event calculated as having a greater than 10,000 year return interval (Robeson 2015). As a result, there were insufficient seeds collected from other resident species in the community to conduct the planted experiment, so seeds of commonly co-occurring species were purchased from S&S Seeds (Carpenteria, California).

This study focuses on only one location and set of populations in California and Spain, respectively. We acknowledge that using only one population from each location may not be representative of all populations of *B. madritensis.* For instance, high genetic and phenotypic diversity has been found across populations in the invaded range of its congener, *Bromus tectorum* (Hufft and Zelikova 2016).

Experimental design

Experiments were conducted in a greenhouse at the University of California, San Diego Biology Field Station in La Jolla, CA, USA. Seeds were planted in cylindrical pots (3.8 cm wide, 18.4 cm deep) containing homogenized local topsoil (Agriservices Inc, Oceanside CA). Seeds from each *B. madritensis* population (Spain and California) were planted both alone and in pairwise competition with resident species from Spain and California (Table 1). Resident species were also grown alone to estimate the competitive effect of *B. madritensis*. Seed planting numbers varied according to pre-estimated germination rates. The seeds of all species were sowed on September 1, 2015. Species did differ in seed germination time thus averaged germination dates for each species were included in the analysis as a trait.

Table 1 Resident species and target species utilized in the experiment, including the abbreviation used in figures, common name, functional group and mean functional traits

Scientific name	Abbrv	Origin	Common name	Functional group	AG biomass (g)	Root mass fraction (g)	Seed mass (g)	Days to germination	Water use efficiency (μmol CO_2 mmol H_2O^{-1})
Avena barbata	AVBA	Spain	Slender wild oat	Annual grass	0.0088	0.8	0.0059	7	2218
Plantago lagopus	PLLA	Spain	Canary grass	Annual forb	0.0029	0.55	0.00028	16	1470
Bromus tectorum	BRTE	Spain	Drooping brome	Annual grass	0.0029	0.84	0.0024	6	7519
Hypochoeris glabra	HYGL	Spain	Smooth cat's ear	Annual forb	0.0015	0.51	0.0006	6	1471
Trifolium cherleri	TRCH	Spain	Cupped clover	Annual forb	0.015	0.53	0.0012	8	2292
Leontodon taraxacoides	LETA	Spain	Lesser hawkbit	Annual forb	0.0039	0.56	0.00037	4	896
Bromus hordeaceus	BRHO	Spain	Soft brome	Annual grass	0.0017	0.89	0.0014	8	9044
Rumex crispus[a]	RUCR	California	Curly dock	Perennial forb	0.008	0.58	0.0037	11	2481
Lasthenia californica	LACA	California	California goldfields	Annual forb	0.0015	0.62	0.0016	20	939
Festuca myuros[a]	FEMY	California	Rat-tail fescue	Annual grass	0.0059	0.63	0.00086	6	20,538
Festuca microstachys	FEMI	California	Pacific fescue	Annual grass	0.003	0.78	0.0015	5	3704
Clarkia purpurea	CLPU	California	Winecup clarkia	Annual grass	0.0049	0.44	0.00035	16	3995
Festuca rubra	FERU	California	Red fescue	Annual grass	0.0052	0.79	0.0011	6	4444
Eschscholzia californica	ESCA	California	California poppy	Perennial forb	0.0036	0.47	0.00018	6	2961
Festuca perennis[a]	FEPE	California	Wild rye	Annual grass	0.014	0.72	0.0047	6	6599
Bromus madritensis	**BRMA**	**California**	**Compact brome**	**Annual grass**	**0.0086**	**0.62**	**0.0017**	**8**	**2937**
Bromus madritensis	**BRMA**	**Spain**	**Compact brome**	**Annual grass**	**0.002**	**0.89**	**0.0018**	**8**	**7883**

AG above ground. Target species highlighted in bold

[a] Listed in the Invasive Plant Inventory for California according to the California Invasive Plant Council. All species are naturalized in California and but with different invasion ratings: *R. crispus*—limited concern, *F. myuros*—moderate concern, and *F. perennis*—moderate concern

Following germination, seedlings were weeded to achieve one seedling per pot (absence of competition) or six seedlings per pot to replicate diffuse competition (interspecific competition, three seedlings of a given resident species and three *B. madritensis* seedlings from the same source location). While this design includes intraspecific competition between both the target and resident species by its very nature, only interspecific competition was measured. Intraspecific competition cannot be separated from the interspecific competition in this design and so was not included in any analyses. There were eight replicates planted for each treatment. The two *B. madritensis* populations were not planted together in competition, nor were *B. madritensis* from Spain planted with resident species from California (nor vice versa) in this experiment.

Above-ground biomass was harvested after 10 weeks, which corresponds to the time from germination to peak biomass for nearby herbaceous communities in Southern California (Cleland et al. 2016). For individuals grown alone, below-ground biomass was also harvested. Above-ground biomass was clipped at soil level. Below-ground biomass was rinsed from the soil over a 1 mm sieve. All samples were dried to a constant mass at 40 °C for 48 h, and weighed to the nearest 0.01 mg.

Competition index

Relative interaction intensity (RII) was calculated from plants grown in competition treatments according to Eqs. 1 and 2 (Armas et al. 2004). This metric is bounded between − 1, representing extreme competition, and + 1, representing strong facilitation.

$$\text{Competitive effect} = \frac{\textit{Biomass of resident grown with B. madritensis} - \textit{biomass of resident grown alone}}{\textit{Biomass of resident grown alone} + \textit{biomass of resident grown with B. madritensis}} \tag{1}$$

$$\textit{Competitive response} = \frac{\textit{Biomass of B. madritensis grown with resident} - \textit{Biomass of B. madritensis grown alone}}{\textit{Biomass of B. madritensis grown alone} + \textit{Biomass of B. madritensis grown with resident}} \tag{2}$$

Traits

Plant functional traits were measured for the invader and resident species, and traits were chosen based on their association with competitive ability, as identified by prior studies. Days to germination is a measure of a seedling's ability to benefit from priority effects where species that establish earlier in the growing season should benefit by sequestering resources first (Sale 1977; Wainwright et al. 2012). Seed mass influences the initial size of the seedling and on seedling provisioning. Consequently, larger seeded species often perform better in competition with other seedlings (Leishman 1999; Turnbull et al. 1999). High water use efficiency can be beneficial to plants facing water stresses but the accompanying decrease in transpiration translates to slowed growth and decreased competitive ability (Drenovsky et al. 2012). Finally, root mass fractions are thought to reflect the differential investment of photosynthates between the aboveground and belowground organs (Titlyanova et al. 1999). For instance, a well-established root can enhance plant recovery from losses of above-ground biomass due to herbivores (Kitajima 1994).

All functional traits were measured on plants grown in the absence of competition. Seed mass and days to germination were measured in pilot trials prior to the experiment. Water-use efficiency was measured as instantaneous gas exchange using a LI-6400 portable gas exchange system (LI-COR, Lincoln, NE, USA). All measures were collected with CO_2 concentration at 400 ppm at an irradiance level of 1500 µmol photons^{-1}. Instantaneous water-use efficiency (WUE) was calculated as the CO_2 assimilation: transpiration ratio. Root mass fraction (RMF) was calculated as root biomass divided by total plant biomass, based on dry weights.

Statistical analyses

All analyses were conducted in R version 3.2.3 (R Core Team 2016). Each metric for relative interaction intensity (competitive effect or competitive response) was predicted with a linear model where origin and resident species were included as fixed effects, and resident species was nested within origin.

Differences between resident species pools in above-ground biomass, WUE, and RMF were assessed with linear models including origin and resident species nested within origin. A separate analysis also assessed differences in these variables between populations of *B. madritensis* of each origin.

Average values for each species were used for days to germination and seed mass because they were collected in a pilot study (Table 1), so we used *t* tests to determine differences in these traits between the resident species pools from California versus Spain.

To evaluate the relative importance of traits versus fitness of resident species in predicting variation in competitive response and effect of *B. madritensis*, we used a model averaging approach (Grueber et al. 2011). The model averaging approach allows us to consider multiple competing hypotheses simultaneously to identify the best set of models according to Akaike's Information Criterion (AIC), by making inferences based on weighted support from multiple models. In traditional multiple regression approaches there are often step-wise approaches used to identify the best model, but this approach is problematic when there is nearly equivalent support for several different models. Using a top model set derived from model averaging as opposed to a single best model can provide a more robust means of obtaining parameter estimates and making predictions, because it can account for model uncertainty (Burnham and Anderson 2003). Separate analyses were constructed for Spain versus California, to explicitly evaluate our hypothesis that fitness effects would be stronger relative to trait differences in the invaded range of *B. madritensis*. The data set used includes five input variables: (1) seed mass, (2) days to germination, (3) root mass fraction (RMF), (4) Water-use efficiency (WUE) and (5) biomass of resident species (fitness).

To generate a sub-model set, we first fit a global general linear model (GGLM; Bates et al. 2015) containing all six variables. Then we standardized the input variables so that the parameter estimates can be interpreted after model averaging (Gelman 2008). Next, we used the dredge function in the *MuMIn* package to consider all combinations of the global model. The dredge function considers all possible combinations of the variables for models. We used get models to select for a subset of those models with an AIC < 4. (Grueber et al. 2011). Finally, we performed model averaging on our top submodels (AIC < 4). We report the conditional estimate results as they are predictions for a factor of interest at the mean of all other parameters (Grueber et al. 2011). We also report relative importance of each variable which can be derived by summing the Akaike weights across all the models in the sets where that variable occurs (Burnham and Anderson 2003).

Results

Trait and fitness differences

The invasive population of *B. madritensis* had higher individual fitness (above-ground biomass) than the native population, when grown under common greenhouse conditions. Specifically, above-ground biomass of *B. madritensis* individuals from Spain was over four times smaller than for individuals from California (Fig. 1: $F_{1,13} = 12.64$, $p = 0.0035$). When one very high value from California was excluded, the result was still highly significant (Fig. 1, Table 2: $F_{1,12} = 29.37$, $p \leq 0.001$). Only one other trait differed between the two populations: RMF was higher for *B. madritensis* from Spain when compared to California (Table 2: $F_{1,13} = 41.78$, $p \leq 0.001$, Online

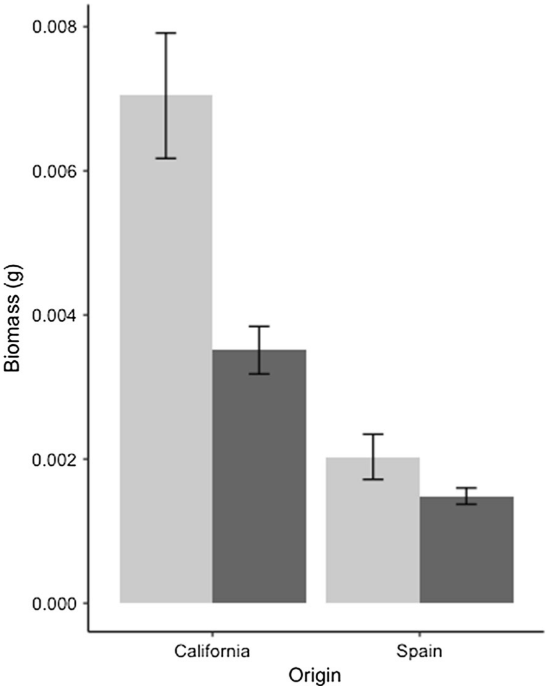

Fig. 1 Above-ground biomass of *B. madritensis* individuals (in grams) from seeds collected in the native range (Spain) and invaded range (California), grown with and without interspecific competition. Light gray is no competition and dark gray is with competition. Error bars indicate 1 ± SE of the mean

Table 2 Functional trait differences between *B. madritensis* (BRMA) collected in California (CA) versus Spain (ES) and between the suites of resident species chosen from California versus Spain

Species	Trait	CA mean	ES mean	SE	(*df*1, *df*2)	F value	*p* value
BRMA	Water-use efficiency	2937	4887	1162	1, 11	2.82	0.12
	Root mass fraction	**0.62**	**0.88**	**0.04**	**1, 13**	**41.8**	**< 0.001**
	Above-ground biomass (g)	**0.007**	**0.002**	**9.2e−4**	**1, 12**	**29.4**	**< 0.001**
	Seed mass (g)	0.0017	0.0018	3.2e−4	1, 8	0.68	0.43
Residents	Water-use efficiency	4439.1	4181.3	948	1, 92	1.07	0.79
	Root mass fraction	0.64	0.69	0.04	1, 92	1.17	0.28
	Seed mass (g)	0.002	0.0019	3.7e−4	1, 92	0.16	0.69
	Above-ground biomass (g)	0.006	0.004	1.3e−3	1, 92	0.81	0.37
	Days to germination	9.21	7.71	0.85	1, 92	1.91	0.17

All values were measured on plants grown in the absence of competition. A separate analysis was performed for each trait. Mean values for seed mass and days to germination were used, based on pilot analyses (measures were not taken on individuals in the experiment). Variation in denominator degrees of freedom (*df*2) for analyses of *B. madritensis* traits reflect removal of outliers (see "Methods" section). Significant terms highlighted in bold

Resource 1). Days to germination was determined by recording days until first germinant for each species. Both populations had similar times to germination in our pilot trial and hence no further analysis was performed (mean values in Table 1).

In our analysis comparing the traits of competing species pools, no measured traits differed significantly between the pool of resident species from California versus Spain (statistical output in Table 2, mean values for each species given in Table 1).

Competitive effect of *B. madritensis* on resident species

Consistent with the predictions of EICA, *B. madritensis* exerted a greater competitive effect on resident species from California than Spain (origin: $F_{1,97} = 14.84$, $p \leq 0.001$, Fig. 2, Table 3), but there was considerable variation in the strength of the competitive effect on resident species (species: $F_{13,97} = 6.96$, $p \leq 0.001$).

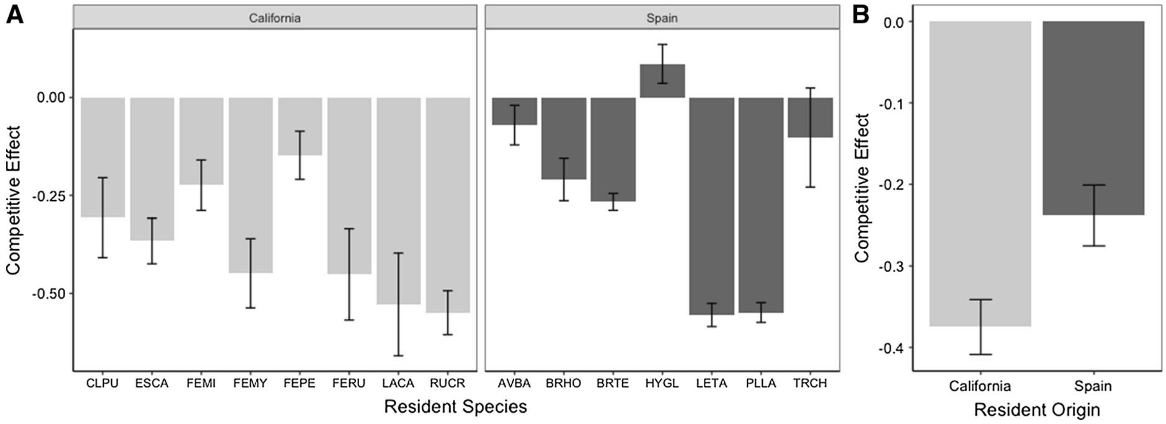

Fig. 2 **a** Competitive effect of *B. madritensis* originating from each population (California or Spain) as measured by the proportional decrease in the biomass of a resident species when in the presence of *B. madritensis* (RII) when grown with each resident species of the same origin from California (dark grey bars) or Spain (light grey bars). **b** Average value of *B. madritensis'* competitive effect on all resident species in each place of origin. Light gray is California and dark gray is Spain. Error bars indicate 1 ± SE of the mean

Table 3 Effects of origin and resident species identity (nested within origin) on competitive response and competitive effect of *B. madritensis*

	Variables	(*df*1, *df*2)	F value	*p* value
Competitive response	**Origin**	**1, 103**	**30.6**	**< 0.001**
	Origin (species)	13, 103	1.81	0.052
Competitive effect	**Origin**	**1, 97**	**14.9**	**< 0.001**
	Origin (species)	**13, 97**	**6.97**	**< 0.001**

Significant terms highlighted in bold

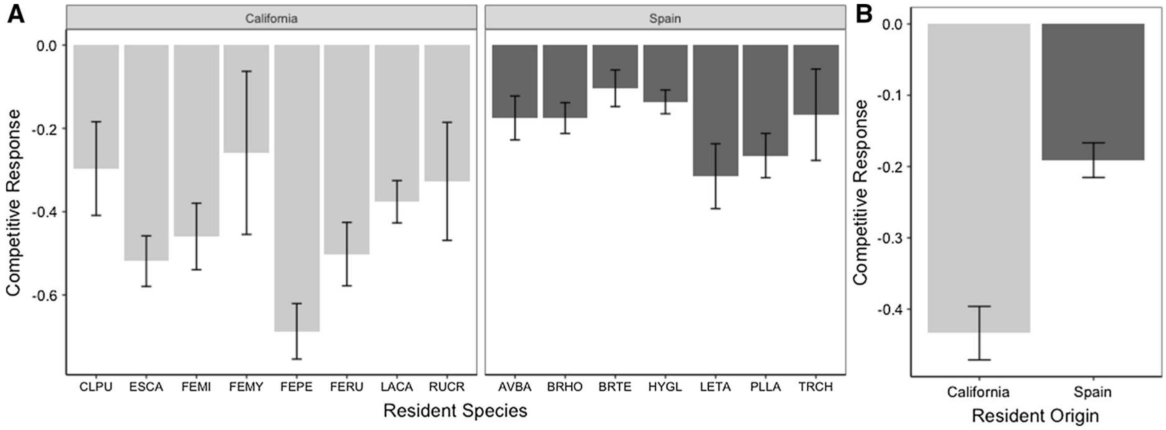

Fig. 3 **a** Competitive response of *B. madritensis* originating from each population (California or Spain) as measured by the proportional decrease in the biomass of *B. madritensis* when in the presence of a resident species (RII) when grown with each resident species of the same origin from California (dark grey bars) or Spain (light grey bars). **b** Average value of *B. madritensis*' competitive response to all resident species tested from each place of origin. Light gray is California and dark gray is Spain. Error bars indicate 1 ± SE of the mean

Competitive response of *B. madritensis* to resident species

Contrary to our initial expectations, *B. madritensis* had a greater reduction in biomass when grown with resident California species (about 40%) compared to when grown with residents of its native Spanish range (25% biomass reduction; origin: $F_{1,103} = 30.6$, $p \leq 0.0001$, Fig. 3a, Table 3). The biomass response of *B. madritensis* to competition again varied depending on the identity of the resident species [origin (species): $F_{13,103} = 1.81$, $p = 0.052$, Fig. 3b, Table 3].

Predicting the strength of competition on the basis of trait and fitness differences

We used model averaging to evaluate the relative importance of traits versus fitness of resident species in predicting variation in competitive response and effect of *B. madritensis*. *B. madritensis* from Spain exerted the strongest competitive effect on resident species from Spain with late germination, higher root mass fraction, low water use efficiency and small seeds ($p < 0.0001$ and importance = 1.00 for all of these traits, Table 4). *B. madritensis* from California exerted the strongest competitive effect on resident species with late germination and small seeds (for these traits $p \leq 0.0001$, importance = 1.00, Table 4).

None of the selected traits predicted competitive responses of *B. madritensis* to growth with resident species from Spain (Table 5). *B. madritensis* collected in California had the greatest response to competition (reduction in biomass) when competing with resident species that had earlier germination times ($p = 0.038$, weighted importance = 0.81, Table 5).

Fitness (above-ground biomass of the resident) was not a significant predictor of variation in the strength of competitive effect or response of *B. madritensis*.

Table 4 The relative importance of resident functional traits for predicting the competitive effect of *B. madritensis* on resident species from Spain or California

Origin	Parameter	Estimate	SE	z-value	*p* value	Relative importance
Spain	(Intercept)	1.7e+00	1.3e−01	12.79	< 0.001	
	Root mass fraction	**− 4.0e+00**	**2.8e−01**	**14.59**	**< 0.001**	**1.00**
	Water use efficiency	**1.6e−04**	**1.2e−05**	**14.08**	**< 0.001**	**1.00**
	Seed mass	**2.0e+02**	**1.3e+01**	**16.07**	**< 0.001**	**1.00**
	Days to germination	**− 1.7e−02**	**3.0e−03**	**5.72**	**< 0.001**	**1.00**
	Comp biomass	− 2.1e+00	3.7e+00	0.57	0.57	0.29
California	(Intercept)	− 2.8e−01	5.7e−02	4.95	< 0.001	
	Root mass fraction	9.6e−03	1.2e−01	0.08	0.93	0.24
	Water use efficiency	− 3.8e−06	2.1e−06	1.84	0.07	0.69
	Seed mass	**2.0e+01**	**7.7e+00**	**2.67**	**0.007**	**1.00**
	Days to germination	**− 1.4e−02**	**2.8e−03**	**5.06**	**< 0.001**	**1.00**
	Comp biomass	8.0e−01	8.8e−01	0.91	0.36	0.33

Fitness in this model is represented by resident species' above-ground biomass (Comp biomass). *SE* adjusted standard error from the model output. Significant terms highlighted in bold

Table 5 The relative importance of resident species functional traits for predicting the competitive response of *B. madritensis* to being grown with each resident species from Spain or California

Origin	Parameter	Estimate	SE	z value	Pr (> |z|)	Relative importance
Spain	(Intercept)	6.0e−02	3.6e−01	0.17	0.87	
	Root mass fraction	8.1e−01	1.0e+00	0.80	0.42	0.45
	Water use efficiency	− 3.9e−05	3.6e−05	1.07	0.29	0.57
	Seed mass	− 4.6e+01	4.2e+01	1.11	0.27	0.48
	Days to germination	2.7e−03	7.2e−03	0.38	0.71	0.20
	Comp biomass	9.5e−01	1.7e+00	0.55	0.58	0.25
California	(Intercept)	− 5.3e−01	2.3e−01	2.33	0.02	
	Root mass fraction	− 2.1e−01	4.2e−01	0.50	0.61	0.23
	Water use efficiency	1.3e−05	8.1e−06	1.58	0.11	0.49
	Seed mass	− 3.2e+01	3.1e+01	1.05	0.30	0.33
	Days to germination	**2.1e−02**	**1.0e−02**	**2.08**	**0.038**	**0.81**
	Comp biomass	− 5.7e+00	4.3e+00	1.32	0.19	0.44

Fitness in this model is represented by resident species' above-ground biomass (Comp biomass). *SE* adjusted standard error from the model output. Significant terms highlighted in bold

Discussion

A major goal of invasion biology is to conduct robust tests of niche-based theories of community assembly, such as the theory of limiting similarity or the EICA hypothesis. While many of our findings were consistent with the predictions of these theories, others were surprising. For instance, *B. madritensis* individuals grown from seeds collected from its invaded range in California grew significantly larger (had higher above-ground biomass) than individuals from seeds collected in the native range in Spain (consistent with EICA). Also consistent with EICA, *B. madritensis* from Spain allocated a smaller proportion of biomass above-ground than individuals from California. Competitive interactions were also stronger between *B. madritensis* and resident species from California; *B. madritensis* had a greater competitive effect on resident species from Californian (consistent with predictions of EICA) as well as a greater competitive response to those species (unexpected based on EICA predictions). Consistent with niche-based theories of community assembly, variation in the competitive effect and response of *B. madritensis* could be predicted by functional traits of the resident species. However, traits were less important for predicting the competitive response than competitive effect of *B. madritensis,* especially for the population of Spanish origin. Fitness did not appear in any model suggesting that the role of fitness in predicting competitive outcomes may be overstated, at least for this species. These findings are discussed in detail below.

Our results show that the invasive population of *B. madritensis* in California achieved larger sizes and allocated a lower proportion of biomass to roots than individuals from its native range, a finding consistent with the EICA hypothesis. For instance, Parker et al.'s (2013) meta-analysis found populations of invasive species to be larger on-average, more abundant and to have higher reproductive outputs in their invaded ranges, although there was significant variation in responses. Several studies have shown that competitive advantages of invasive species are associated with changes in biomass allocation, not just individual size (Meyer and Hull-Sanders 2008; Morrison and Mauck 2007; Pattison et al. 1998; Wilsey and Polley 2006). In our study, the decreased biomass allocation to roots in the invasive population of *B. madritensis* may be associated with adaptations to higher soil resource levels or increased light competition in the invaded range (Iwasa and Roughgarden 1984; Poorter et al. 2012).

The differences in size and traits of *B. madritensis* populations likely contributed to the variation in competitive interactions we observed. Notably, competitive interactions were stronger between *B. madritensis* and resident species from its invaded range; the biomass of both *B. madritensis* and its resident species from California were reduced by twice as much when grown together than biomass reductions observed for the Spanish communities. These competitive effect results support our hypothesis that *B. madritensis* should exert stronger competitive effects on species in its invaded than native range. Our findings also support past studies showing that competitive effects of invasive species on species in their introduced ranges are generally stronger than on those in their native ranges (Ni et al. 2010; Vila and Weiner 2004). In contrast, our finding that *B. madritensis* was more competitively suppressed by Californian than Spanish residents (as measured by resident species abilities to suppress its growth) was unexpected, and potentially suggests that community assembly processes in Californian communities select for species and genotypes with stronger competitive abilities. These results support the conclusion that the invasion of *B. madritensis* into California is not due to weaker competitive resistance of the California resident communities than are found in Spain. It is worth noting, however, that studies of other invaders have come to the opposite conclusions (see for example Callaway et al. 2011) suggesting that biogeographic variation in competition intensity can vary by system and species.

While we originally hypothesized that both traits and fitness would contribute to invader success of *B. madritensis,* fitness was noticeably absent from predictors of competitive effect and responses in both ranges. Despite the large difference in biomass between native and introduced populations of *B. madritensis*, no models included fitness of resident species as a significant predictor of competitive outcomes, suggesting that community assembly in this system is more strongly mediated by traits than fitness differences among competing species. Our results are consistent with prior studies predicting that species traits can predict the impact of invasions (MacDougall et al. 2009; Pyšek et al. 2012), and that trait-derived competitive hierarchies are better predictors of competitive interactions than size-based fitness hierarchies (Kraft et al. 2014; Kunstler et al. 2012) even in invaded systems (Lai et al. 2015). To our knowledge, however, this is the first example of a trait-based competitive hierarchy in the competitive interactions of species in their native versus invaded ranges, uniquely allowing us to draw conclusions about the specific traits likely to predict invasion success in this system.

Our experiment showed that both competitive effects and responses of *B. madritensis* were predicted by traits, but those traits differed between the invaded and native ranges. Further, although competitive effect and response were both stronger in California, we found variation in the suite of traits predictive of competitive effect versus response, as was initially predicted by Goldberg (1990). Only one trait was predictive of the competitive response of *B. madritensis*, and only in California. Early germination was the best predictor of a negative competitive response of *B. madritensis* to being grown in competition with resident species from California, a result consistent with restoration experiments showing that areas seeded with early germinating native species had the lowest rates of invasion by early-germinating exotic species such as *B. madritensis* (Cleland et al. 2013). In contrast, multiple traits predicted the competitive effect of *B. madritensis* on resident species. *B. madritensis* had the greatest competitive effect on species with late germination and small seeds, in both California and Spain. Species that germinate later in the growing season can be competitively suppressed by earlier active species that can pre-empt space and resources (Wainwright et al. 2012), and smaller seeded species have lower provisioning to support initial life stages. This suggests that native species with these traits are most likely to be negatively impacted by highly competitive invading species, and offers a potential way for land managers to predict native species that might be important conservation priorities in areas at risk of invasion.

In Spain, species with low water use efficiency and high allocation to roots were also more negatively impacted by competition with *B. madritensis*. It is interesting to note that traits had greater predictive power to explain variation in the competitive effect of *B. madritensis* in its native than invaded range, and potentially suggests a greater signal of trait-based community assembly in that system. In highly invaded areas such as Southern California, multiple invasions could alter environmental niche space and cause a kind of "disassembly" process (Reynolds et al. 2017), weakening the signal of trait-based community assembly. Further, these results highlight that the traits predicting competitive effect and response can differ in key ways that deserve future investigation.

As with any experiment ours has some important caveats. First, resident biomass in this study was defined by above-ground biomass, and differences we observed in root allocation of *B. madritensis* between its native and invaded ranges suggests that root competition could be important for understanding its success as an invader. Second, our resident pools included both native and naturalized non-native species. While done to maximize the realism of our results, quantifying competitive interactions with representative species pools, our results need to be interpreted carefully, as they are not a comparison of native and non-native species, but rather one invader and "resident" species, regardless of origin. Similarly, in this study we focused on competitive effect and response of our focal invader, *B. madritensis.* However, we did not focus on competitive effects and responses of each resident species; studies on the competitive effects and responses of residents would be ideal for identifying species to plant in restoration projects that are minimally effected by competition from invasive species. Finally, our competitive species pool included both annual and perennial species, but our experiment was limited to the first growing season following germination; competition between an annual species like *B. madritensis* and a perennial species can, of course, change over time. Another study in California showed that that native perennial species are competitively suppressed as seedlings by annual invading species, but in later years the relationship flips, and perennial species can competitively suppress annuals (Goldstein and Suding 2014). An interesting next step to this study would be to examine if similar relationship changes occur over time as well.

In conclusion, this study aimed to determine the relative roles of functional traits and fitness differences for predicting both the initial response of an invader to competition with residents, and the initial competitive effect of the invader on common resident species. Overall, these results indicate that competitive interactions of *B. madritensis* in its native and invaded ranges are driven by functional traits rather than fitness differences although there may be other factors at play environmentally since fitness did not appear in any of our models. We propose that trait based community assembly processes are likely to vary in strength with biogeography. This study shows that different suites of traits may aid in identifying those native species likely to strongly compete with invaders, versus those that will be competitively suppressed by invaders, with important implications for invasion control efforts by land managers. We suggest that future competition experiments consider the context dependent nature of the effect of different traits on competition as it relates to invasions.

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Chapter 2

Drought in Southern California coastal sage scrub reduces herbaceous biomass of exotic species more than native species, but exotic growth recovers quickly when drought ends

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Drought in Southern California coastal sage scrub reduces herbaceous biomass of exotic species more than native species, but exotic growth recovers quickly when drought ends

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Abstract Semi-arid regions with Mediterranean-type climates harbor exceptional biodiversity, but are increasingly threatened by invading exotic annual species and climatic changes, including drought. In semi-arid ecosystems, antecedent conditions often influence plant growth, but the role of antecedent conditions for drought response and recovery of native versus exotic species remains largely unexplored. From 2013 to 2016, we imposed experimental rainfall treatments (average rainfall, moderate or severe drought) in plots under a native shrub canopy and in inter-spaces dominated by herbaceous vegetation, and quantified growth (peak biomass) and abundance (cover) of native and exotic herbaceous species. The following year, we quantified recovery from the drought treatments (2017). Exotic biomass was less resistant to drought (declined more than native biomass), but was more resilient (increased more than native biomass in the year following drought), especially in unshaded inter-spaces between shrubs. These responses were associated with life history; annual species responded more negatively to drought in the inter-spaces than perennial species. Current years' rainfall was a better predictor of biomass than prior rainfall, but antecedent factors were also important. After four years of rainfall treatments, exotic species had the highest growth recovery in the severe drought treatment, while growth of natives had the opposite response. In contrast, litter was positively associated with plant growth regardless of origin. This study demonstrates that when native and exotic species differ in life history, as they do in Mediterranean climate ecosystems, they may respond differently to antecedent factors, and hence differ in recovery from climate extremes such as drought.

Keywords Antecedent conditions · Ecological resilience · Invasion · Litter · Seedbank

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Introduction

The California floristic province is a global biodiversity hotspot with high rates of endemism, especially in the Mediterranean climate region of the state (Cincotta et al. 2000). This region is also at risk for species' loss due to invasion by exotic species (Seabloom et al. 2006; Underwood et al. 2009) and climate change (Loarie et al. 2009; Harrison et al. 2015). Significant climate change is predicted for this region in the coming decades (Cayan et al. 2008; Diffenbaugh and Giorgi 2012), including drought (Seager et al. 2007; Diffenbaugh et al. 2015) and increased interannual variability in rainfall (Berg and Hall 2015; Yoon et al. 2015). Local-scale studies often observe that high rainfall increases the growth or abundance of exotic annuals (Hobbs et al. 2007; Ashbacher and Cleland 2015). Meta-analyses have shown that invasive species often have higher leaf area and growth rates than non-invasive species (Van Kleunen et al. 2010), as well as traits associated with higher water demand (Cavaleri and Sack 2010). Accordingly, exotic invasive species often have higher performance under conditions of high resource availability (including water) than native species (Daehler 2003). Similarly, recent meta-analyses have found that exotic species tended to respond more negatively to drought than native species (Sorte et al. 2013; Liu et al. 2017). Together these studies suggest that drought should impact growth of native species less than exotic species.

However, regional models project that some exotic annual grasses in the semi-arid regions of the Western U.S. will expand their ranges with declining rainfall (Bradley 2009). One way that drought might promote invasion is by reducing native biomass, thus reducing competition for light, and soil resources, and benefiting fast-establishing invasive exotic species in subsequent years with higher rainfall (Jiménez et al. 2011; Diez et al. 2012). Drought can also promote fire (Dennison et al. 2014), and positive feedbacks by facilitating exotic grass invasion, fine fuel accumulation, and hence accelerated fire regimes (D'Antonio and Vitousek 1992; Balch et al. 2013). Given the impacts of invasions on ecosystem processes and biodiversity (Liao et al. 2008; Ehrenfeld 2010; Powell et al. 2011; Vilà et al. 2011), it is critical to better understand how invasion by exotic species will influence ecosystem responses to drought and interannual rainfall variation in this region.

Most of the studies evaluating variation among functional groups in their response to drought have focused on relationships with rainfall in the most recent growing season. However, antecedent environmental conditions can play a large role in predicting ecological processes, resulting in a time lag in correlations between environmental conditions and plant growth (Ogle et al. 2015). For instance, plant growth and production can be influenced by rainfall in prior years, in addition to the current year (Lauenroth and Sala 1992; Sala et al. 2012). Prior years' rainfall is particularly important for understanding growth dynamics in semi-arid systems, including grasslands (Oesterheld et al. 2001) and shrublands (Anderson and Inouye 2001). In semi-arid systems, high rainfall can increase seed bank abundance (Holmgren et al. 2006; Dudney et al. 2017) and perennial meristems (Reichmann et al. 2013), contributing to an increase in plant growth in the following year. However, following a year of high production, standing litter can increase soil shading, which can have either positive or negative effects on seedling establishment, growth, and community-level production in subsequent years (Facelli and Pickett 1991; Wolkovich et al. 2010). Prior work in herbaceous-dominated ecosystems has shown that plant functional groups vary in response to antecedent conditions (Dudney et al. 2017), and resilience following drought (Hoover et al. 2014), but few studies have investigated how native versus exotic species vary in this respect. In notable exceptions, Concilio et al. (2016) found that introduced cool-season species responded more to antecedent rainfall than native species in a semi-arid grassland in Colorado, and Potts et al. (2006) found differing responses of ecosystem carbon flux to antecedent conditions depending on whether native or invasive species dominated. However, it remains unclear whether the results of these initial studies are transferrable to other regions and vegetation types.

Here, we evaluated the drought response and recovery of biomass and abundance (cover) of native and exotic herbaceous species, as well as the role of antecedent conditions in these responses. We conducted our research in Californian coastal sage scrub (CSS), a semi-arid ecosystem traditionally dominated by drought deciduous shrubs and diverse herbaceous species (Rundel 2007; Cleland et al. 2016). However, CSS is increasingly invaded, especially by exotic annual species (Minnich and Dezzani 1998). Soils in CSS can harbor a large seedbank of exotic annual species, enabling these exotic species to establish quickly following disturbance (Cox and Allen 2008). In Southern California, nitrogen deposition and accelerating fire frequency in CSS have been associated with type-conversion from shrubland to grassland dominated by exotic annual species (Talluto and Suding 2008). Hence, we evaluated how herbaceous species responded to drought under the shrub canopy, as well as in the inter-spaces between shrubs, the two contexts where herbaceous species are found in this system. As with other Mediterranean climate ecosystems (Funk et al. 2016), invading species are more likely to be annual than perennial in this system. Hence, it is important to note that the differential responses of native and exotic species in this system are likely tied to life history differences, and associated variation in growth and response to resource variation (Chapin 1980; Grime 1977; Tilman 1985).

From 2012 to 2016, California experienced the most severe drought in millennia (Griffin and Anchukaitis 2014; Robeson 2015). During these 4 years, we maintained a rainfall manipulation experiment (average rainfall, moderate or severe drought treatments) in adjacent plots either under a native shrub canopy or in inter-spaces dominated by herbaceous vegetation, and then ceased treatments and monitored biomass during the first high rainfall year following the drought (2017). We expected that (1) exotic species growth would decline more with drought than native species, because exotic species in this system are mostly annual and have a suite of traits including fast growth but low tolerance for moisture stress. We further expected that (2) biomass of both native and exotic species in the recovery year following drought would depend on antecedent factors such as rainfall in prior years, abundance of seeds in the seedbank, and standing litter from prior years' biomass. A synthesis of long-term observations in the United States found that annual species were more sensitive than perennial species to interannual rainfall variability (Cleland et al. 2013), thus we expected that biomass of annual exotic species would be more sensitive to these antecedent factors than biomass of perennial native species. In contrast, we expected that (3) the seedbank would be of greater importance for understanding the response of native biomass to drought compared to exotic biomass, where seeds of native species would be more abundant in the seedbank following drought than seeds of exotic species, as has been found elsewhere in California (LaForgia et al. 2018). Finally, we expected that (4) antecedent factors could play different roles in drought recovery of herbaceous biomass under the shrub canopy than in the shrub inter-spaces, given that shade and antecedent factors such as litter accumulation under the shrub canopy could potentially buffer plants from desiccation under drought conditions.

Methods

A rainfall manipulation experiment was conducted from 2012 to 2017 in the Santa Margarita Ecological Reserve (33°29′N, 117°09′W) located at the Riverside-San Diego county line, California, USA. The site has a Mediterranean climate with cool, wet winters and hot, dry summers. Growing seasons in this analysis are defined by the timing of winter rains which typically occur from October to April, with peak biomass occurring in the spring of each year. Throughout the manuscript growing seasons are referenced by the year in which peak biomass occurred; i.e. the 2013 growing season spanned October 2012 to April 2013.

This site was ideal for evaluating how species composition influences ecosystem responses to drought, because all experimental plots had similar starting soils, aspect, and disturbance history (D. Lipson, unpublished data). The experimental site was a grazed pasture prior to the establishment of the Reserve in 1962, when grazing ceased. The area was then patchily re-colonized by two co-dominant native shrubs: *Salvia mellifera* (black sage) and *Artemisia californica* (California sagebrush), with a sparse understory containing both native and exotic herbaceous species. Shrub inter-spaces were dominated by exotic species such as *Bromus madritensis* (Spanish brome) and *Centaurea melitensis* (Maltese star thistle), but included native species such as *Stipa pulchra* (purple needle grass) and *Dichelostemma capitatum* (blue dicks). Terminology for referring to species origin varies widely (Richardson et al. 2000); throughout this manuscript we refer to all species not native to California as exotic for brevity. We list all species found in the experimental plots, including invasive status of exotic species according to the California Invasive Plant Council, in Supplementary Table 1

Within the site 36 plots were established; six shelter-control plots were uncovered (3 shrub dominated, 3 inter-spaces), while 30 treatment plots were covered with a clear, polycarbonate roof (approximately 1.6 m higher than the ground surface, slanted to allow runoff) which permitted light transmission but intercepted all rainfall during the growing season. Shelter control plots received ambient rainfall, the same amount of rainfall applied to the 100% treatment plots (which had shelter tops). Thus, these plots were not meant as controls for the rainfall treatment, but rather as controls for unintended effects of the experimental infrastructure.

The rainfall shelter tops were 3.5 × 3.5 m^2, but all measurements were made in a central 3 × 3 m^2 plot (0.5 m buffer from the edge). Half of the plots were centered on mature *S. mellifera* shrubs with *A. californica* as a less abundant component of the vegetation (here-after referred to as "shrub understory" plots), while the remaining plots were in shrub inter-spaces dominated by herbaceous vegetation (here-after "open" for brevity). Shrub understory and open plots were paired spatially to reduce bias associated with any unmeasured environmental gradients at the site, at least one meter apart, with paired plots having the same rainfall treatment. The site was nearly flat (little slope); rainfall treatments did not run off of target plots and hence trenching was not necessary between plots. Supplementary Fig1a shows a photograph of the rainfall shelters at the field site, and Supplementary Fig1b shows an aerial view of the spatial arrangement of the plots.

Rainfall shelters were established over treatment plots prior to the 2013 growing season, and roof tops were removed during the dry summer months to permit light penetration and cleaning (and reattached prior to the fall rains). During the growing season, the shelters prevented all ambient rainfall from falling on the plots. All rainfall was collected using a gutter system and held in large storage tanks; experimental rainfall treatments were applied with irrigation on the first dry day following a rain event. Rainfall quantity applied to the experimental treatments was calculated from local weather station data. Rain events exceeding 18 mm were split into multiple application days to reduce surface water run-off from plots.

Three rainfall manipulation treatments were applied during the experiment: 50%, 100% or 150% of ambient rainfall (shrub vs open x three rainfall treatments x five replicates + six non-covered controls = 36 plots). Due to the intense drought which occurred from 2012 to 2016, the 150% rainfall treatment was similar to long-term average precipitation at the site (Fig. 1). Hence, throughout the manuscript we refer to all treatments occurring during the experimental phase of the study as experimental drought treatments (150% treatment approximating "average rainfall," while the 100% and 50% treatments represent moderate and severe drought, respectively).

The rainout shelters were removed following the 2016 growing season, and all plots received ambient rainfall during the 2017 growing season (a higher than average year), to assess the potential for resilience following drought. Growing season (October through April) rainfall totals are shown in Fig. 1 for the last 30 years, including the treatment amounts in the experimental years. Precipitation at the experimental site was measured by the "Fallbrook 5 NE CA US" NOAA weather station for growing season years 2009–2017 (www.wrcc.dri.edu). Prior to the 2009 growing season the "Vista, CA US" station used as the closest station with historic data, 23 km away from the newer Fallbrook station.

Above-ground biomass was collected from a 20 cm × 50 cm area within each plot (0.1 m^2) in April, the time of peak growing season biomass, in each of the five growing seasons (four years of rainfall manipulation, and one recovery year where all plots received ambient rainfall). Harvest locations were marked with stakes to prevent re-harvesting in subsequent years. All above-ground biomass of plants rooted in the area was clipped at the soil level—including live biomass as well as recently senesced biomass that reflected current year's growth. All litter, defined as dead plant material from previous growing seasons, was also collected in the harvest area. In the shrub understory, herbaceous biomass harvest areas were positioned to avoid main stems of perennial shrubs, but occasionally contained small shrub seedlings. Biomass in each plot was identified and sorted in the field into three categories: exotic biomass, native biomass, or litter. Biomass samples were dried to a constant mass at 40°C for 72 h in the laboratory and weighed to the nearest 0.01 mg. Woody biomass

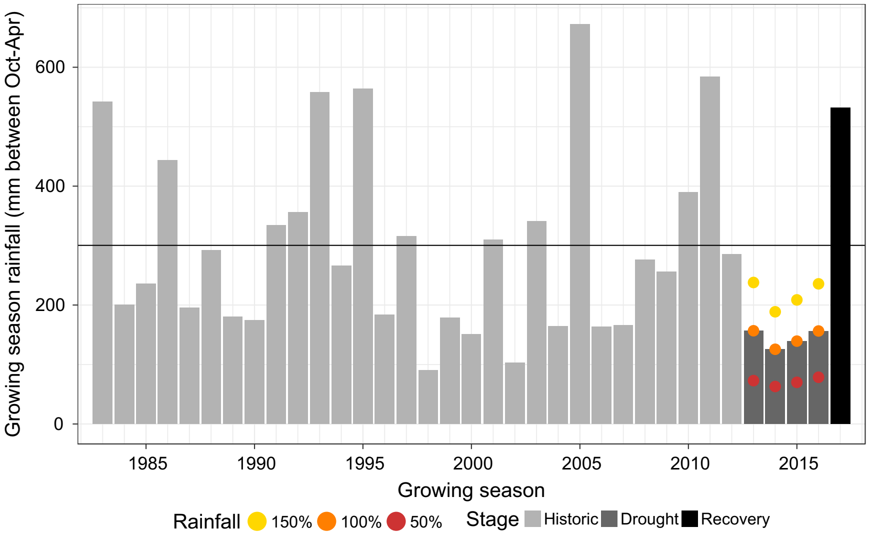

Fig. 1 Growing season precipitation (October–April) at the experimental site over the last 30 years. Growing season year indicates the year when peak biomass occurs (April). Bar color indicates experimental stage (light gray = historic, dark gray = experimental drought, black = recovery). Rainfall amount experimentally applied during the 4-year manipulative phase of the experiment are shown as circles: yellow = 150% ambient rainfall (average rainfall), orange = 100% (moderate drought), = 50% (severe drought). The historic 30-year average (1983–2012 growing seasons) at the site is shown as a horizontal line (299 mm)

production of mature shrubs was not quantified. Estimates of above-ground photosynthetic biomass production (integrating across shrub-dominated and herbaceous vegetation) based on normalized difference vegetation index (NDVI) are published elsewhere (Esch 2017), and are consistent with the patterns of herbaceous biomass presented in this analysis.

Biomass is a relevant metric for understanding the impact of species composition on ecosystem-level processes. However, we did not sort biomass to species, and hence we analyzed change in species' abundances in permanent plots to evaluate how life history (annual versus perennial) influenced species' drought response and recovery. In April, for each of the five growing seasons, we visually estimated percent cover of each species within a central 1 × 1 m^2 plot marked with permanent metal stakes at the four corners, with a maximum value of 100. When there were overlapping individuals total cover could sum to more than 100. We summed the percent cover of all annual vs perennial species, and separately all native versus exotic species, within each plot. Only understory species were included to mirror the biomass analysis, hence shrub cover was not included in this analysis.

After rainfall manipulations ended, the seed bank was sampled in October 2016 (prior to the onset of the 2017 growing season rains). A 5 cm × 10 cm area of soil was excavated to a depth of 5 cm, along with any litter on the soil surface, adjacent to the area harvested for biomass in April 2016. The collected soil was spread in a thin layer over commercial potting soil in germination trays (30 × 15 × 5 cm) in the UC San Diego Biology Field Station greenhouses, watered daily to keep soil moist and monitored for the identity and abundance of germinating seedlings for a period of 6 months. The total number of germinating seeds was calculated as a measure of seed bank abundance for native versus exotic species. A summary of the experimental design is shown in Fig. 2, and additional detailed methods are described in Esch (2017).

Statistical analyses

All analyses were conducted in R version 3.2.3 (R Core Development Team 2016). Initial analyses of biomass and cover in the 2013–2016 growing seasons were conducted with general linear mixed models

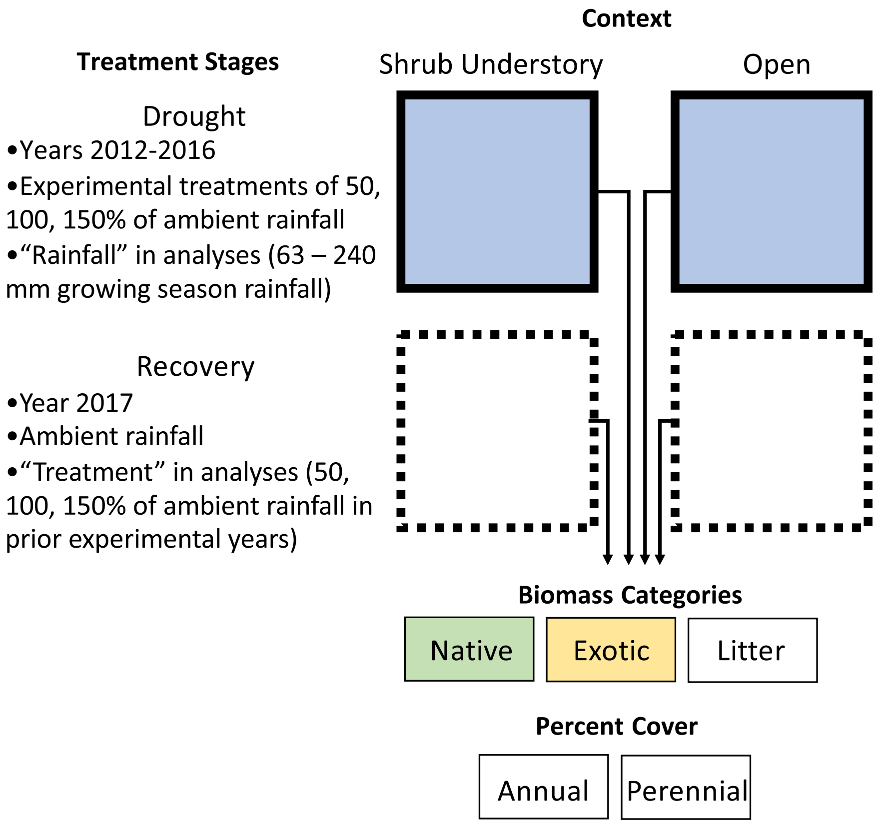

Fig. 2 Conceptual figure of the experimental design. Plots were covered with clear rainout shelters (indicated by light blue color) during years with rainfall manipulation (drought stage, 2013–2016). During the drought stage plots were experimentally given 50%, 100%, or 150% of ambient rainfall. In the recovery stage, all plots were uncovered and exposed to ambient rainfall (white). In all years, the herbaceous biomass from the shrub understory and open plots was harvested and sorted into exotic biomass (yellow), native biomass (green), or litter (white)

using the *lme* call in the package *nlme* (Pinheiro et al, 2013). These models included growing season rainfall (continuous), species origin, and their interactions; plot was included as a random factor to account for the repeated-measures design across years. The influence of life-history differences was evaluated in a separate model, where percent cover was predicted by rainfall (continuous), life history (annual versus perennial), and their interactions (biomass was only separated by species origin, and hence could not be analyzed for life-history differences). Data from the shrub understory versus open plots were analyzed in separate models. As described in the results below, the initial analysis revealed that biomass was influenced by species origin x rainfall interactions. Hence, native and exotic biomass were subsequently analyzed in separate models to facilitate the interpretation of complex statistical interactions. Significance for each factor was evaluated with Type II Wald chi-square tests using the *Anova* function in the *car* package (Fox and Weisberg 2011).

To evaluate the influence of antecedent effects (litter and previous year rainfall) in addition to the current year's rainfall, we used a model averaging approach (Grueber et al. 2011). This approach is useful in cases such as ours where wished to evaluate the relative weight of models with and without antecedent effects. We used Akaike's Information criteria (AIC) to determine the support for each individual model in a set of models. The potential input variables were (i) litter mass (ii) current year's rainfall and (iii) previous year's rainfall. To generate a sub-model set, we first fit a global general linear mixed model (Bates et al. 2014) containing all three variables. We standardized the input variables using the *stdize* function in the *MuMIn* package, so that the parameter estimates could compared among factors with different measurement scales after model averaging (Gelman 2008). Next, we used the *dredge* function in the *MuMIn* package to consider all combinations of the global model (Bartoń 2016). We used *get.models* to select a subset of those models which varied by AIC < 4, performed model averaging on these top submodels, and reported the conditional estimate results (following the procedure of Grueber et al. 2011).

In keeping with the structure of the prior analyses, the number of individuals emerging from the seed bank was analyzed separately between shrub understory and open plots. Here, we used a linear model including species origin and experimental drought treatment (as 50%, 100%, or 150% of ambient rainfall, continuous) as fixed factors.

Resilience of biomass in the recovery year (2017) was analyzed using a set of steps similar to the drought response analyses. Biomass in 2017 was first analyzed in a linear model where species origin, previous drought treatment (50%, 100%, or 150% of ambient rainfall) and their interaction were included as fixed factors, with separate models for shrub understory versus open plots. Given species origin by treatment interactions (see "Results"), the subsequent analysis of antecedent effects was conducted separately for native versus exotic biomass to enable a mechanistic evaluation of the statistical interactions. Again the role of antecedent factors in drought recovery (previous year's rainfall, standing litter, and number of germinants in the 2016 seedbank) was assessed with a model averaging approach, using the same methods previously described for the analysis of drought response.

Results

Site community composition and shelter controls

A total of 43 species were recorded in our analyses of percent cover across all plots and years in this experiment (Supplementary Table 1). Seventeen of the 24 native species were perennial, while 15 of the 19 species of exotic origin were annual (Table 1), reflecting a key difference in the dominant life-strategies of native versus exotic species in this system. In contrast there were not major morphological differences between origin groups; both native and exotic cover was approximately equally comprised of grasses and forbs (data not shown). Exotic species dominated the herbaceous community in this system, representing approximately 3/4 of both cover and biomass (Table 1).

Biomass of native and exotic species were compared between the unsheltered controls and the sheltered 100% plots, which both received the same amount of rainfall. There was no difference between the control and 100% rainfall plots for native biomass, nor for exotic biomass in the shrub understory, but in the open there was greater exotic biomass in the unsheltered controls than in the 100% rainfall plots (Supplementary Fig. 2). All rainfall treatment plots had shelter tops, and hence relative responses of biomass to the drought treatments can be compared across treatments. However, we proceed with the caveat that absolute values of exotic biomass presented in the manuscript are lower than would be observed in the absence of the shelters.

Drought response and recovery

The rainfall manipulation experiment corresponded with the lowest period of rainfall on record for our site, and our lowest rainfall treatments represented a severe 4-year drought (Fig. 1). Consistent with expectations, plant growth (peak season biomass) declined in response to our drought treatments, but with differences between native and exotic species which depended on context (shrub understory versus open vegetation). In the open plots, exotic biomass declined more with drought than native biomass (significant Rainfall × Origin interaction, Table 2). However, in the shrub understory exotic and native biomass had similar declines in response to drought (significant main effect of Rainfall, Table 2). Overall, there was lower herbaceous biomass in the shrub understory than in the open areas, and exotic and native biomass were more equally represented in the shrub understory, while exotic biomass dominated in the open herbaceous plots (compare Fig. 3 A vs B).

During the recovery year (2017), all plots received some of the highest rainfall on record at the experimental site (Fig. 1). In the open plots, native and exotic biomass differed in the dynamics of their recovery following the secession of drought

Table 1 Summary of community composition averaged across all experimental plots during the 5-year experiment, including species origin (native or exotic to California), life history (annual or perennial), mean total cover (summed cover within each group, can be greater than 100%), fraction of total cover (proportion of total cover made up by each group, sums to 1), species richness, and mean total herbaceous biomass (note that biomass was not sorted into annual versus perennial species, so this represents total exotic or native biomass, averaged across all plots)

Origin	Life history	Mean total % Cover	Fraction of total cover	Species richness	Mean herbaceous biomass (g/m^2)
Exotic	Annual	97.9	0.72	15	31.71
	Perennial	7.4	0.05	4	
Native	Annual	5.7	0.04	7	7.50
	Perennial	24.6	0.18	17	

Table 2 Statistics from linear models evaluating how species origin (native/exotic) and rainfall influenced herbaceous biomass during four years of experimental rainfall manipulation (response during 2013–2016 growing seasons, top), and in the recovery year (2017 growing season bottom)

Timeframe	Context		χ^2	*df*	*p* value
Response to drought (2013–2016)	Open	**Rainfall**	**56.6**	**1**	**< 0.001**
		Origin	**41.6**	**1**	**< 0.001**
		Rainfall:Origin	**33.1**	**1**	**< 0.001**
	Shrub understory	**Rainfall**	**6.69**	**1**	**0.009**
		Origin	2.88	1	0.09[a]
		Rainfall:Origin	0.29	1	0.59
Recovery (2017)	Open	Treatment	0.60	1	0.45
		Origin	**53.1**	**1**	**< 0.001**
		Treatment:Origin	**5.05**	**1**	**0.033**
	Shrub understory	Treatment	0.73	1	0.40
		Origin	2.07	1	0.16
		Treatment:Origin	0.37	1	0.54

Rainfall is treated as a continuous variable in these analyses, because the experimental drought treatments resulted in different total growing season rainfall amounts among years. The multi-year analysis of response to drought included plot as a random repeated factor, and hence the mixed model analysis of deviance statistic is presented as χ^2. Note that in the recovery year (2017) all plots received the same rainfall, and hence the model term indicating the experimental rainfall treatment in the prior year is abbreviated as "Treatment." Significant terms are highlighted in bold

[a] Indicates marginal significance

treatments (Treatment x Origin interaction, Table 2). Open plots that had previously experienced drought treatments had lower native biomass, but higher exotic biomass, compared to plots that had received the highest rainfall treatment (Fig. 3 C). In contrast, in the shrub understory, the prior rainfall treatments did not influence growth of native or exotic species in the recovery year (Fig. 3 D).

The drought response and recovery of percent cover by species origin were similar to those for biomass (Supplementary Fig. 3), and for the sake of brevity are not discussed in the main text.

The influence of antecedent factors in drought response

During the drought, current rainfall was the most important predictor of biomass, and there were few significant influences of antecedent factors (Table 3); for instance, previous year's rainfall did not influence native or exotic biomass. However, in the open plots,

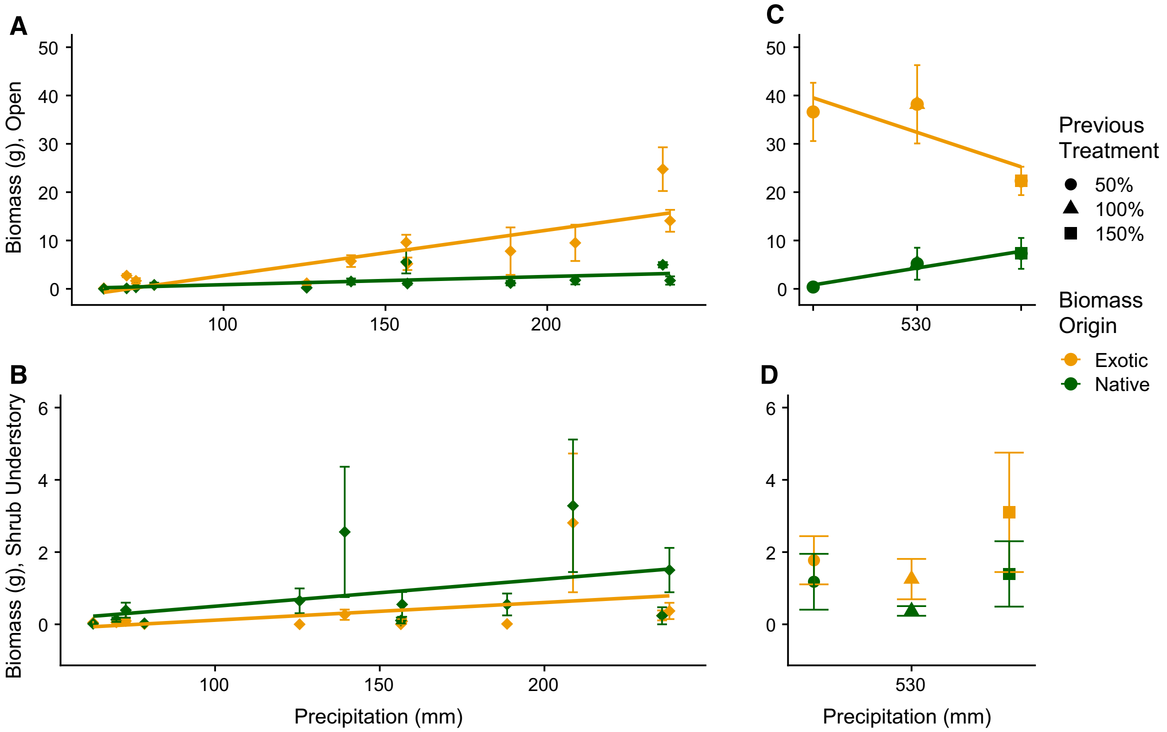

Fig. 3 Herbaceous biomass versus total growing season rainfall during the experimental drought (2013–2016, **a**, **b**) and recovery (2017, **c**, **d**) stages. Biomass was sorted to exotic (yellow) or native (green) origin, and quantified in both in open plots (**a**, **b**) and in the shrub understory (**c**, **d**). Means (n = 5) and ±1 SE of the mean are shown. Shape in the recovery year (**c**, **d**) indicates previous rainfall treatment: square =50% of ambient rainfall (severe drought), circle = 100% (moderate drought), triangle = 150% (average rainfall). Note different range of values on the vertical axes

standing litter from the previous growing season had a positive effect on exotic biomass during drought (Table 3). In the shrub understory, both native and exotic biomass had a positive relationship with current rainfall, but no antecedent factors were important predictors.

Abundance of native and exotic species in the seedbank following drought

Of the 1095 seedlings which emerged in the greenhouse from our field-collected soils, we were able to identify just over half to the species-level and hence identify the seedling as either of native or exotic origin (566 seedlings). Species identified from the seedbank are indicated in Table S1, and accounted for 70% of total species cover observed in the experiment. Early mortality of emerging seedlings limited our ability to identify remaining seedlings. There was a greater mean number of seedlings germinating in soils collected from open plots compared to soils collected under the shrub understory (Fig. 4), and exotic seedlings dominated the open plots while native species were more common in the shrub understory (marginally significant main effects of Origin, Table 4). In soils from open plots, there was a significant Origin × Treatment interaction (Table 4), whereby exotic seedling abundance was lowest in plots that had experienced the drought treatments, but native seedling abundance did not vary with treatment. A visual examination of the total number of germinating individuals (identified to species plus unidentified) reveals very similar overall patterns of seedbank responses to prior rainfall treatments (Supplementary Fig. 4), suggesting the dynamics of the identified species reflect the overall seedbank responses, with the caveat that individual species dynamics in the unidentified pool could have differed significantly from the identified species.

Table 3 Biomass responses to drought treatments (2012–2016) as influenced by both concurrent and antecedent factors

Context	Biomass		Estimate	SE	*z* value	*p* value	Importance value
	Type	Model term					
Open	Native	**Rainfall**	**1.8E−02**	**4.1E−03**	**4.42**	**< 0.001**	**1**
		Previous Rainfall	− 4.7E−03	3.0E−03	1.53	0.13	0.52
		Litter	1.4E−02	1.3E−02	1.13	0.26	0.38
	Exotic	**Rainfall**	**9.4E−02**	**1.3E−02**	**7.09**	**<0.001**	**1**
		Previous Rainfall	− 7.3E−03	1.1E−02	0.67	0.50	0.28
		Litter	**1.2E−01**	**4.6E−02**	**2.57**	**0.01**	**1**
Shrub understory	Native	**Rainfall**	**4.7E−03**	**1.8E−03**	**2.57**	**0.01**	0.92
		Previous Rainfall	1.8E-03	1.6−03	1.17	0.24	0.41
		Litter	− 2.7E-03	2.3E−03	1.16	0.25	0.36
	Exotic	**Rainfall**	**2.2E-03**	**1.0E−03**	**2.15**	**0.03**	0.89
		Previous Rainfall	− 3.7E−04	8.7E−04	0.42	0.67	0.18
		Litter	8.6E−04	1.4E−03	0.62	0.53	0.2

This table shows the output from a model averaging analysis evaluating the relative importance of growing season rainfall (Rainfall), growing season rainfall in the previous year (Previous Rainfall), and Litter for predicting native and exotic herbaceous biomass in open plots versus in the shrub understory. SE=Adjusted standard error from the model output

Significant treatment effects are highlighted in bold

The influence of antecedent factors in drought recovery

As described previously, exotic and native biomass in the open plots had opposing relationships with prior rainfall treatments in recovery year, as evidenced by a Rainfall x Origin interaction (Table 2, Fig. 2c). To investigate the influence of antecedent factors, native versus exotic biomass were analyzed separately using a model averaging approach including prior rainfall treatment, litter, and seedbank abundance as continuous variables. In the open plots, prior rainfall treatment had a significant positive effect on native biomass, but a negative effect on exotic biomass (Table 5). Litter mass remaining in plots from the prior year's plant growth had a significant, positive effect on native biomass in both open plots and in the shrub understory (Table 5).

The influence of life history on drought response and recovery

Total percent cover also declined in response to the drought treatments, but differed between annual and perennial species and depended on context (shrub understory versus open vegetation). In the open plots, annual species' percent cover declined more with drought than perennial species (significant Rainfall x Life history interaction, Table 6). However, in the shrub understory neither life history nor rainfall treatment explained significant variation in percent cover (Table 6). Overall, there was lower cover of annual species in the shrub understory than in the open plots, and cover of perennial species was higher in the shrub understory than in the open plots (compare Fig. 5a vs b). These responses of annual versus perennial cover to drought are nearly identical to responses of exotic versus native cover (Supplementary Fig3), and biomass (Fig. 2a, b), demonstrating the important role of life history for understanding the drought responses of native versus exotic species in this system.

However, during the recovery year (2017), the dynamics of annual versus perennial cover were not predicted by differences in species origin. In the open plots, annual cover was greater than perennial cover overall (main effect of Life history, Table 6), but the cover of both annual and perennial species was negatively impacted by prior drought severity (main effect of Treatment Table 6, Fig. 5c). In contrast, the

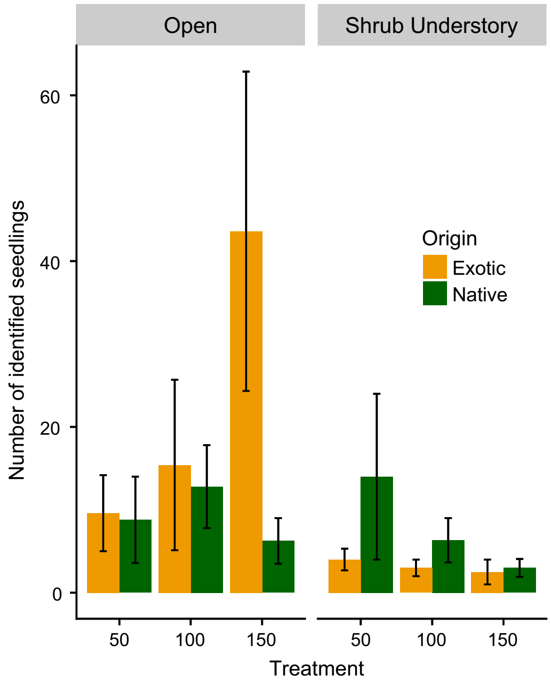

Fig. 4 Number of germinating individuals from soils collected in October 2016, following 4 years of experimental drought treatments. Only individuals that could be identified to the species level are included, according to the species origin as exotic (yellow) or native (green). Soils were collected from both the shrub understory (left panel) and open plots (right panel)

Table 4 Statistics from linear models evaluating how native versus exotic origin (Origin) and experimental drought treatments (Treatment) influenced variance in the abundance of germinating seeds from the seedbank, for soils collected in October 2016, following four growing seasons

Context	Factor	*F* value	*df*	*p* value
Open	Treatment	2.93	1	0.13
	Origin	2.53	1	0.08
	Treatment:Origin	**3.32**	**1**	**0.03**
Shrub understory	Treatment	2.35	1	0.15
	Origin	2.24	1	0.09
	Treatment:Origin	5.25	1	0.25

Significant terms are indicated in bold font

responses of exotic versus native biomass to drought from 2013–2016 were nearly identical to the cover responses of annual versus perennial species, respectively (compare Figs. 2a and 5a). In the shrub understory plots, neither rainfall nor life history had a significant effect on species percent cover, again highlighting how context influenced species recovery from drought.

Discussion

Temporal dynamics have long been at the core of community ecology theory, both for predicting species coexistence, and changes in community composition in response to variation in the environment (e.g. Holling 1973; Sousa 1984; Chesson 1994). These theories are ever more relevant as ecologists seek to predict how ecosystems will respond to an increasingly variable global climate (Collins et al. 2013), and continued introductions of exotic species (Bellard et al. 2013; Seebens et al. 2015). The response of an ecological system to a disturbance, such as severe drought, is often defined in terms of resistance and resilience—the magnitude of the response compared to baseline conditions and how quickly the system recovers to the pre-disturbance state, respectively (Holling 1973; Westman 1978). In this experiment, we found that native biomass was more resistant to drought, but exotic biomass was more resilient. The response of exotic biomass to drought was strongly driven by life history, with annual cover also responding negatively to drought. The drought recovery of exotic species was not explained by life history, however, because annual and perennial species had similar patterns of drought recovery. We also found that context played an important role, where drought response and recovery were more influenced by rainfall in open plots than in the shrub understory. Antecedent factors were also more important in open plots, and sometimes differed in their influence on native versus exotic species. For instance, in the recovery year, prior rainfall treatment was a positive predictor of native biomass, but a negative predictor of exotic biomass, only in the open plots. In contrast, litter was an antecedent factor that tended to influence native and exotic biomass in the same way, albeit at different times. Litter from the prior year's growth had a positive effect on exotic biomass in the open plots during the response year, and on native biomass in the recovery year regardless of context. These findings will be detailed in the remainder of the discussion.

In the open plots, exotic biomass and abundance (as estimated by cover) declined more steeply than native biomass in response to drought, consistent with the

Table 5 Recovery following drought (2017) as influenced by both concurrent and antecedent factors

Context	Biomass		Estimate	SE	*z* value	*p* value	Importance value
	Type	Model term					
Open	Native	**Litter**	**6.3E−01**	**1.7E−01**	**3.66**	**<0.001**	**1**
		Treatment	**7.9E−02**	**1.4E−02**	**5.75**	**<0.001**	**1**
		Seedbank	1.5E−02	3.0E−02	0.49	0.63	0.27
	Exotic	Litter	7.9E−01	4.5E−01	1.75	0.08	0.62
		Treatment	**− 1.6E−01**	**3.8E−02**	**4.31**	**<0.001**	**1**
		Seedbank	1.2E−01	7.9E-02	1.49	0.14	0.51
Shrub understory	Native	**Litter**	**2.3E−02**	**7.0E−03**	**3.25**	**0.001**	**1**
		Treatment	4.7E−03	5.5E−03	0.85	0.39	0.31
		Seedbank	− 7.1E−02	5.5E−02	1.29	0.19	0.43
	Exotic	Litter	3.4E−03	7.5E−03	0.46	0.65	0.18
		Treatment	− 7.7E−04	5.8E−03	0.13	0.89	0.16
		Seedbank	− 1.1E−02	5.3E−02	0.20	0.84	0.16

This table shows the output from a model averaging analysis evaluating the roles of 2013–2016 growing season experimental rainfall treatment (Treatment), grams/m^2 standing dead litter (Litter), and the number of germinating seeds in the seedbank in October 2016 (seedbank) for predicting native and exotic herbaceous biomass following drought in open plots versus in the shrub understory

Significant terms are indicated in bold font

Table 6 Statistics from linear models evaluating how species life history (annual/perennial) and rainfall influenced percent cover during 4 years of experimental rainfall manipulation (response during 2013–2016 growing seasons, top), and in the recovery year (2017 growing season bottom)

Timeframe	Context	Model term	Sum Sq	*Df*	*F* value	*p* value
Response to drought (2013–2016)	Open	**Rainfall**	**5093**	**1**	**47.57**	**< 0.001**
		Life history	**3446**	**1**	**32.19**	**< 0.001**
		Rainfall:Life	**2273**	**1**	**21.24**	**< 0.001**
	Shrub understory	Rainfall	25.02	1	1.55	0.23
		Life history	1.77	1	0.11	0.74
		Rainfall:Life	59.42	1	3.68	0.07[a]
Recovery (2017)	Open	**Treatment**	**163.1**	**1**	**95.3**	**0.01**
		Life history	**1926**	**1**	**1125**	**< 0.001**
		Treatment:Life	5.34	1	3.12	0.22
	Shrub understory	Treatment	0.64	1	0.36	0.61
		Life history	0.011	1	0.01	0.94
		Treatment:Life	0.36	1	0.20	0.69

Rainfall is treated as a continuous variable in these analyses, because the experimental drought treatments resulted in different total growing season rainfall amounts among years. Note that in the recovery year (2017) all plots received the same rainfall, and hence the model term indicating the experimental rainfall treatment in the prior year is abbreviated as Treatment

Significant terms are highlighted in bold

[a] Indicates marginal significance

findings of recent meta-analyses of experimental rainfall reduction (Sorte et al. 2013; Liu et al. 2017). Our result is also consistent with other experiments and observations showing a reduction in the abundance of exotic herbaceous species in response to drought in California (Copeland et al. 2016).

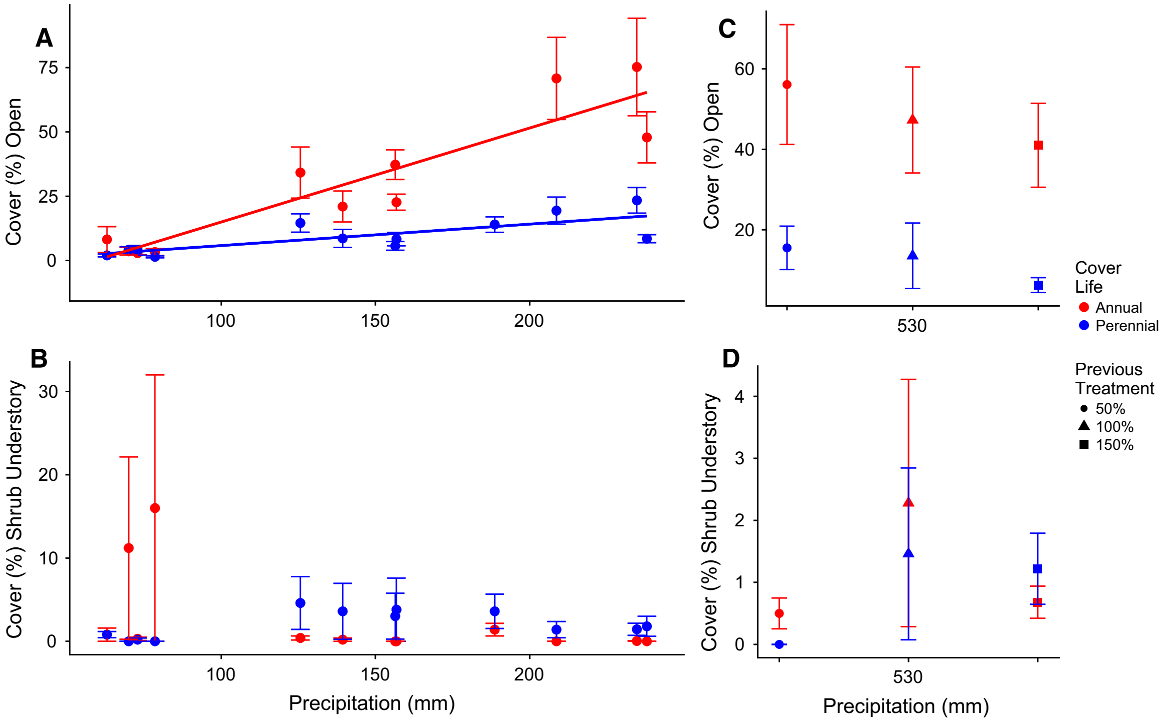

Fig. 5 Species percent cover in response to precipitation amount during the experimental drought (2013–2016, **a**, **b**) and recovery year (2017, **c**, **d**). Color indicates summed percent cover of annual (blue) or perennial (red) species, in open plots (A, B) and in the shrub understory (**c**, **d**). Means (n = 5) and ±1 SE of the mean are shown

However, in the first high-rainfall year following drought, exotic biomass rebounded from nearly absent to the highest levels observed during the experiment. It is possible that exotic seeds remaining in the soil following drought were able to produce large individuals in the high-rainfall year of 2017, a kind of demographic inertia that is especially beneficial to species in variable environments. Drought can increase resources (including space) by reducing the growth of resident vegetation, enabling fast-growing annual, exotic species to quickly establish when favorable growing conditions return (Jiménez et al. 2011; Diez et al. 2012). Consistent with this prediction, Kimball et al. (2014) found that extreme drought following fire prevented native shrub re-establishment, and ultimately facilitated conversion of coastal sage scrub to an herbaceous, invaded vegetation type.

Our finding that exotic biomass was more sensitive to drought than native biomass is strongly associated with the dominant life histories of the two groups. When we analyzed the percent cover responses of annual versus perennial species, we saw that their responses were nearly identical to those of exotic versus native species, respectively. Our results are consistent with prior work showing that across herbaceous-dominated ecosystems in the United States, annual species are more sensitive to interannual variation in rainfall than perennial species (Cleland et al. 2013). This also suggests that our results are likely to be relevant for other Mediterranean-type ecosystems, where annuals dominate exotic species pools (Funk et al. 2016).

We found mixed responses of biomass to antecedent rainfall; during the years of drought, prior rainfall did not influence biomass, but in the recovery year native and exotic biomass had opposing relationships with prior rainfall. A recent meta-analysis found a signal of lagged rainfall effects across an aridity gradient from deserts to mesic grasslands, where prior year's rainfall was proportionally more important for predicting production in wet sites (Sala et al. 2012). Therefore, our site may be on the dry end of a gradient where prior year's rainfall is less important than current year's rainfall for influencing plant growth.

However, their analysis did not distinguish among functional groups, which can respond differently to drought. For instance, an experimentally severe drought in a tall-grass prairie reduced productivity overall, but impacted dominant forbs more than dominant grasses (Hoover et al. 2014). The grasses rebounded following drought due to a strong demographic effect, resulting in a persistent shift in community composition. The Sala et al. (2012) analysis also did not include other antecedent factors such as litter accumulation, which could be correlated with prior year's rainfall but be more mechanistically predictive.

Standing litter had a positive effect on exotic biomass during the drought, and on native biomass in the recovery year. Although litter tended to have a similar influence on native and exotic biomass in our study, litter is likely to have differing influences on growth and abundance among species. For instance, Dudney et al. (2017) found that high annual rainfall increased litter in the following year, suppressing forb growth but increasing grasses, resulting in stronger lagged precipitation effects on forbs. Litter can modify germination rates (Reynolds et al. 2001), reduce light (Foster and Gross 1998), protect seedlings from herbivory (Facelli and Pickett 1991), and increase soil moisture (Wolkovich et al. 2010). Hence, litter accumulation can be a key mechanism linking previous year's rainfall to shifts in production and species composition in the following years. A recent meta-analysis found a positive relationship between litter and new biomass production across common garden experiments, but a neutral relationship in field experiments (Loydi et al. 2013). Interestingly, field studies in dry sites tend to find a positive relationship between litter and new biomass production (Boeken and Orenstein 2001; Eckstein et al. 2012), suggesting that the influence of litter on plant growth is likely context dependent. At our semi-arid site shade, protection from herbivory or increased soil moisture may underlie the positive relationship between litter and biomass we observed in this experiment.

In the open plots, the number of exotic seedlings emerging from the seedbank was positively associated with prior rainfall treatments, and hence the seedbank could not explain the dramatic recovery of exotic biomass in plots that had experienced the drought treatments. In contrast in the shrub understory, we found a trend towards greater abundance of native germinants in plots that had experienced drought compared to plots that had experienced average rainfall, even though native biomass showed the greatest recovery following the average rainfall treatments. This potentially suggests that native species, at least in the shrub understory, did not break dormancy during the prolonged drought, and seeds accumulated over this time. La Forgia et al. (2018) found accumulation of dormant seeds during drought of native forbs but not exotic grasses, in a more mesic system in Northern California. Capacity for persistence in soil is common in species with variable reproductive success across years (Pake and Venable 1996), and persistent seed banks are common in the Mediterranean-climate regions of California that experience high-interannual variability in rainfall (Parker and Kelly 1989). Few studies have compared the dynamics of native versus exotic seedbanks (but see Faist et al. 2013; Gioria and Pyšek 2016). However, we might expect native species to have longer lived seedbanks than exotic species in this system for two reasons; first, exotic species often germinate faster, and across a wider array of environmental conditions, compared with native species (Chrobock et al. 2011; Wilsey et al. 2011; Wainwright and Cleland 2013), and hence would not be expected to leave a persistent seed bank. Second, exotic grasses in California have larger seeds than native grasses (Sandel and Dangremond 2012), and large seeded species have lower persistence in the seedbank (Rees 1994). However, the generality of this finding will depend on differences in seed size between native and exotic species, and are likely to vary across systems because of observed latitudinal and regional variation in seed size (Moles et al. 2008). We should also note the important caveat that nearly half of the emerging seedlings suffered mortality before they could be identified, a common issue in seedbank studies that limits our ability to say with certainty how seedbank abundance is related to species percent cover observed at the end of the growing season.

Given that neither litter nor the seedbank could mechanistically predict the positive influence of prior drought on exotic biomass in the recovery year, what mechanism might have been responsible? One possibility is nitrogen accumulation due to reduced plant uptake or decreased leaching losses during the drought; a recent meta-analysis of rainfall reduction experiments showed that inorganic nitrogen, especially ammonium, can accumulate under dry conditions (Homyak et al. 2017). Consistent with this hypothesis, inorganic nitrogen accumulated more over time in our drought treatments than the treatments receiving higher rainfall (Castro 2018). This suggests that the increase in exotic biomass following severe drought in our experiment may have been caused by high-nutrient availability. For instance, nitrogen enrichment often promotes invasion by fast-growing exotic species (e.g. Huenneke et al. 1990; Bobbink et al. 2010), especially annuals (Suding et al. 2005). A study in Northern California found that exotic growth was only promoted by high rainfall on fertile sites and in the absence of competitors (Eskelinen and Harrison 2014), highlighting how exotic growth in our experiment could be promoted by high rainfall after a period of drought during which nitrogen accumulated in soil. While not directly testable in this experimental design, drought may have also altered competitive interactions between native and exotic species; shifting species interactions (Suttle et al. 2007) could cause shifts in community-level responses to environmental change, such as the ones observed in this study.

One of the most striking findings of this study is how dynamics of biomass and cover in the shaded understory of the native shrubs differed from the responses in the open, herbaceous-dominated plots. In the understory, native and exotic biomass declined to the same degree with drought, and also recovered to the same extent in 2017. Biomass in the shrub understory was made up equally of native and exotic species, and exotic biomass was markedly lower than in the open plots; potentially reflecting reduced levels of competition for soil resources between native and exotic species in the low-light conditions of the shrub understory (Soliveres et al. 2011). This suggests that dynamics of resistance and resilience in response to drought may be dampened in stressful or low-resource environments, and is a promising avenue for future research. This also suggests that as shrub-dominated habitats are increasingly converted to exotic annual grassland, as a result of global changes such as accelerating fire regimes, nitrogen deposition (Talluto and Suding 2008) and drought (Kimball et al. 2014), we could expect to see a shift in the dynamics of drought response and recovery in these systems, whereby ecosystem biomass production dominated by exotic annual species is increasingly sensitive to interannual variation in rainfall.

In conclusion, we found that exotic biomass declined steeply in response to our imposed severe drought, but recovered in the first year of high rainfall, to levels higher than in experimental treatments that had maintained close to average rainfall at the site. This result is strongly associated with the life histories of the dominant exotic (mostly annual) versus native (mostly perennial) species in this system. Our results are likely to extend to other Mediterranean-type ecosystems where annual species dominate the exotic species pool (Funk et al. 2016). Our results also suggest that predicted increases in interannual rainfall variability (drought followed by high rainfall) could further promote growth of exotic species in this system, particularly in open areas where shrub canopy is sparse. We also found that antecedent factors, specifically seedbank abundance and litter from the prior year's production, differed in their influence on native versus exotic biomass depending on spatial context (shrub understory versus open plots for seed bank) or temporal context (during or following drought for litter). Together these results demonstrate how temporal variability in rainfall differentially influences growth and abundance of native versus exotic species, with important ramifications for ecosystem dynamics and biodiversity in this diverse region.

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Chapter 2, in full, is a reprint of the material as it appears in:Puritty CE, Esch EH, Castro SP, Ryan EM, Lipson DA, Cleland EE (2019) Drought in Southern California coastal sage scrub reduces herbaceous biomass of exotic species more than native species, but exotic growth recovers quickly when drought ends. Plant Ecology 220:151-169. The dissertation author was the primary investigator and author of this paper.

Chapter 3

Legacy of severe drought shifts ecosystem towards later phenology during recovery

Abstract:

Understanding the effects of inter-annual climate variability on ecosystem functioning is increasingly important in the context of global climate change. Species have distinct reactions to variable climate conditions and thus feedbacks associated with shifting species composition represent a key source of uncertainty in predicting ecosystem responses to climate extremes. From 2013 to 2016, we imposed experimental rainfall treatments (average rainfall, moderate or severe drought) in plots under a native shrub canopy and in open inter-spaces dominated by herbaceous vegetation, and quantified growth (peak biomass) and abundance (cover) of native and exotic herbaceous species. The following year, we quantified recovery from the drought treatments (2017) and evaluated species specific and community weighted phenology traits. We found that the open plots dominated by herbaceous vegetation under the most severe drought exhibited higher abundances of species with longer blooming phenology in the recovery year as compared to the ambient or moderate drought plots. We found that ecosystem level phenology on these plots mirrored the species composition in that these plots also displayed delayed seasonal phenology. This study demonstrates that drought can impact ecosystem level phenology by having a multi-year legacy on shifting community composition and function.

Introduction:

The ecological and functional consequences of extreme climate events and the predictors of ecosystem response and recovery remain a key interest for ecologists due to their variability. (Smith 2011). Inter-annual climate variability and extreme weather events cause shifts in community composition because of the differential responses of species (De Boeck et al. 2018). Unfortunately, our understanding of how extreme weather events influence biodiversity and ecosystem functioning beyond productivity remains limited (Jentsch and

Beierkuhnlein 2008). The invasion of functionally distinct species creates a mixed cover system which is known to increase the complexity of predicted ecosystem level responses (House et al. 2003; Scanlon et al. 2005). Recognizing how climate dynamics will influence species interactions in an invaded system both during and after a disturbance event is particularly salient. Phenological shifts are particularly important to understand as they influence not only plant interactions, but also pollinator cues, carbon uptake and other ecosystem processes in such a way that they can have wide ranging impacts on the ecosystem as a whole (Brody 1997; Dunne et al. 2003; Rathcke and Lacey 1985). We know that the effects of a drought can have both direct and legacy or lagged effects on community composition (De Boeck et al. 2018; Wiegand et al. 2004) but whether these shifts result in changes in community level functioning and phenology following drought is unclear.

It is crucial to understand how these lagged effects or legacies of drought on community composition work in conjunction with the direct effects of drought for a broad awareness of how ecosystems change in response to climate variability. In a central USA grassland, researchers found that the differential effects of drought on dominant grasses versus forbs contributed to a shift in species abundances in the plant community, although annual net primary productivity (ANPP) recovery was not affected (Hoover et al. 2014). Other studies exploring community response to climate extremes show minimal effects at the ecosystem level (i.e. productivity) (Jentsch et al. 2011; Kreyling et al. 2008). However, comparable studies show dramatic shifts in ecosystem function and structure during recovery. Quantifying the differential response of vegetation to disturbance is integral to informing how an ecosystem will respond to invasion by functionally distinct exotic species.

Climate driven shifts in community composition can be neutral, shifting species abundances but not ecosystem level processes, but they also can influence large scale shifts that change ecosystem function (De Boeck et al. 2018; Jentsch et al. 2009). Alternate state theory posits that ecosystems are self-organizing and driven by biotic and abiotic interactions. The self-organizing characteristic of ecosystem dynamics says that areas can support multiple, stable species assemblages that represent alternate states with unique feedback cycles (Suding and Hobbs 2009). These ecosystem feedbacks either maintain a persistent state in the ecosystem or cause transitions to other alternate states (Briske et al. 2006). These processes are particularly important to understand in an invaded system as there is potential for a feedback loop that favors exotic species, only further endangering native communities and shifting ecosystem function. The impacts of invasion on community function likely impact both the drought period as well as the recovery stage.

Evidence that the influence of drought on productivity and community composition continues following drought leads us to believe that phenology could be influenced following drought as well (Cleland et al. 2007; Jentsch et al. 2009; Ogaya and Peñuelas 2003). Shifts in plant phenology resulting from drought and alternations in community composition could have implications beyond ecosystem functions as they could disrupt plant-plant relationships as well as any relationships with herbivores, fungi, pollinators etc (Brody 1997; Dunne et al. 2003; Rathcke and Lacey 1985). Previous studies exploring the effects of global change on plant phenology have largely focused on warming (Menzel et al. 2006) where researchers have showed that earlier flowering species are more sensitive to warming (Dunne et al. 2003). However, they also showed that the phenological response of a community to extreme weather events is context dependent upon the functional diversity of a plot (Jentsch et al. 2009).

We know that drought impacts productivity and has the potential to shift ecosystem function but how drought effects community level phenology of more complex mixed cover systems is unknown.

Southern California is home to a large scale ecological invasion where native largely perennial and shrub based plant communities have been increasingly encroached upon by exotic annual grasses and herbs (Cleland et al. 2016). Following their introduction some 250 years ago (Watson 1880), these grasses now cover nearly 10 million hectares of the state of California (D'Antonio and Vitousek 1992). The woodier native communities are characterized by their slow growth which bolsters their resistance to drought (Kolb and Davis 1994) and shading from shrub cover that reduces competition and limits community composition shifts (Soliveres et al. 2011). Alternatively, herbaceous exotic species exhibit earlier phenologies (Cleland et al. 2015; Wainwright et al. 2012) and their communities are characterized by fast growth (Van Kleunen et al. 2010) and an increased ability to rebound after drought (Daehler 2003; Puritty et al. 2019) so that community composition shifts are more common when these species are present. The presence of these grasses has caused several shifts in ecosystem functioning such as nutrient cycling and has increased the frequency of wildfires (Balch et al. 2013; D'Antonio and Vitousek 1992). Furthermore, the county of San Diego in southern California is a biodiversity hotspot, which is characterized by many rare and endemic species (Cincotta et al. 2000; Myers et al. 2000). Because of these species small population sizes and patchy presence, they are at increased risk of being out competed by exotic species and lost to extinction as a result of the on-going invasion. Climate change models predict an increase in variability in Southern California climates with both increased droughts and drought severity (Cayan et al. 2008;

Diffenbaugh et al. 2008) combined with an increase in the frequency and magnitude of wet years (Berg and Hall 2015; Yoon et al. 2015).

In previous studies, we found that in our system of invaded Southern California ecosystem, drought shifts biomass, community composition and productivity during drought (Puritty et al. 2019). However, we found little evidence for shifts in phenology aside from a lengthening of the growing season for shrub dominated plots. Following drought, our system demonstrated a legacy of community composition shifts favoring exotic annual species. This result caused us to ask whether community level phenology demonstrated a lagged effect from drought since a direct effect was not apparent. We asked the following question: Do drought driven shifts in community composition influence ecosystem level phenology following drought? To answer this, we measured productivity and species abundances following the cessation of a controlled precipitation experiment in the field combined with species specific phenological traits measured in a common garden experiment to determine the presence of any ecosystem level phenology shifts and if we could identify any species driving those patterns.

Methods

We conducted a controlled precipitation experiment at Santa Margarita Ecological Reserve (SMER; 33°29′N, 117°09′W) located at the Riverside-San Diego county line, California, USA. The site has a Mediterranean climate with cool, wet winters and hot, dry summers. The site was subjected to the California drought that started in 2012. Within the field site 30 plots had been established, each 3 x 3 meters square. Half of the plots were dominated by the native shrubs *Artemisia californica* (California sagebrush) and *Salvia mellifera* (black sage). We refer to these as the shrub cover or shrub understory plots. The other half of the plots were open and dominated by exotic herbaceous species such as *Bromus madritensis* and

Centaurea melitensis. The native and exotic dominated plots were paired spatially - the entire area had been a grazed pasture but when the reserve was established grazing ceased, and native shrubs re-colonized the area. Hence, both native and exotic-dominated plots had a similar soil, aspect, and disturbance history.

Rainout shelters were established over all plots prior to the 2012/13 growing season covered with a clear, polycarbonate roof permitting light transmission but intercepting all rainfall during the growing season. All rainfall was collected using a gutter system and stored in large tanks and then reapplied via irrigation. Three rainfall manipulation treatments applied during the experiment: ambient (100% of rainfall re-applied with irrigation), drought (50% of ambient), and high water (150% of ambient). The control plots did not have rainout shelters and received 100% of rainfall. Due to the naturally intense drought which occurred in this region the "high" rainfall treatment was similar to long-term average precipitation at the site. During the duration of the 2012-2014 drought the average yearly rainfall was 19.3 cm when compared to the 100-year average of 40.6 cm (www.wrcc.dri.edu). The year following that extreme drought (2015/16) brought 25.4 cm of rainfall. Finally, the growing season of 2016/17 delivered the end of the drought bringing 55.1cm of precipitation. Hence, throughout the manuscript the 150% rainfall treatment is referred to as "normal rainfall," the 100% treatment is termed "drought" and the 50% treatment is termed "severe drought." The rainout shelters were removed following the 2015-2016 growing season, and all plots received natural rainfall during the 2016-2017 growing season, to assess the potential for resilience following drought. All data pertaining to this chapter were collected during this time. During the 2016/2017 growing season (December 2016-July 2017) we monitored plot level productivity, and species abundances.

Species level phenology

In the late spring/early summer of 2017, we collected seeds from 10 common species at SMER (Table 1) to screen them for individual phenological traits including time to germination, growing season duration, and time to peak biomass. Together these species average about 70% of cover on control plots. This experiment was conducted in a field plot at the UC San Diego Biology Field Station in La Jolla, CA, USA. Each species was planted in monoculture at a density of 5g of seed/m^2 in circle plots with a diameter 0.25 m each (0.255g of seed/0.051m^2). There were 5 replicates of each species and they were planted in a randomized block design. Germination was monitored daily until all plots had germinanted, while NDVI measures to assess growing season duration and time to beak biomass were taken bi-weekly for all plots until senescence. Monocultures were unfenced and hence open to herbivory. The diameter of the crop scan measurement is half of the height it is being measured from. We constructed a PVC pipe stand that was 0.5m off the ground to ensure that all measurements were taken from the same height.

Predictive power of phenology traits

In order to evaluate species specific drought response and recovery, we analyzed change in species' abundances in permanent plots. In April 2016 (last year of drought) and April 2017 (first year of recovery), we visually estimated percent cover of each species within a central 1 x 1 m^2 plot marked with permanent metal stakes at the four corners. We laid a PVC grid of the same size to ensure the area was uniform on all plots. For this measure we estimated the number of 10 x 10 cm grid cells within the 1 m^2 plot which was occupied by each species, for a maximum of 100. Each species was evaluated separately, so when multiple species occupied grid cells, or there were overlapping individuals at the top and bottom of the canopy, then total cover could sum to more than 100.

Traits

We also had measures of community level flower phenology consisting of bloom season time of year (mean), duration of bloom season, bloom season start, and bloom season finish from a California database on wild plants (calflora.org). We translated the growing season to a numeric system where the beginning of the season (October) was 1 and the end of the season (September) was ranked 12.

Ecosystem level phenology

We collected data on plot level productivity at SMER from January 2017- June 2017. The most commonly used remotely sensed indicator of plant productivity is the normalized difference vegetation index (NDVI) (Rouse Jr, Haas et al. 1974). We used a Multispectral Radiometer (MSR5) interfacing with a Data Logger Controller (DLC) from CROPSCAN Inc. which measures reflectance readings to measure NDVI. The MSR5 is attached to a pole that is held 1.5m above each plot for measurements. Because of the size of our plots, we measured NDVI at the four corners of each plot and then took the mean of those measures to calculate the plot level productivity. We took each measurement 0.5m in from the edge of the plot to avoid any edge effects in the data. Measurements were all conducted on sunny or partly cloudy days as cloud cover compromises the data. Measurements were taken every 10 days, weather permitting, to document the green-up and senescence of each plot.

Statistical Analysis

All analyses were conducted in R version 3.2.3 (R Core Development Team 2016).

We used species abundances and the phenology traits (Table 1) to calculate community weighted means for each trait, plot, and year. We first calculated the total abundance of all species in each plot (not always 100%) and divided the abundance of each species in each plot by the total abundance of species on that plot to calculate a relative abundance for each species. Then we multiplied the species relative abundances by each trait value, and summed to get community weighted mean trait values for each plot, trait, and year. Analyses predicting each community weighted trait mean were conducted with general linear mixed models using the lme call in the package nlme (Pinheiro *et al.*, 2013). These models included drought treatment, year, and their interactions; plot was included as a random factor, and accounted for the repeated-measures design across years. If year was significant, we analyzed each year (2016 drought, 2017 recovery) separately with models including only treatment and plot as a random factor.

For the NDVI data, we first calculated the raw NDVI from the difference of the wavelengths 680 from 800 divided by the combined wavelength measures of 800 +680. This standardized the measure across all plots and treatments. We then subtracted 0.18 from the raw NDVI measurements to standardize between the two instruments and calculate the NDVI data for the analysis. The following procedure was used to remove outliers. The ddply function from the plyr package (Wickham 2011) was used to calculate the mean, standard deviation, standard error as well as quantiles for the top and bottom quarters of the NDVI data. NDVI values were removed that exceeded 1.5 times the upper and lower quantiles. Mean NDVI for each plot on each day was based on the average of the within plot replicates, calculated after outlier removal. To evaluate how treatments and plot types differed in canopy greenness, we ran linear models for each date to predict plot NDVI based on treatment, community composition and their interactions on NDVI.

The difference in the ecosystem level phenology of each treatment was calculated from the average of the highest 5 NDVI values (greenness) for each plot. A linear model was run for each date during the season where greenness was predicted on the basis of treatment, community type and their interaction.

Results

Species level phenology

We intended to run the same analysis for difference in productivity peaks for the BFS experiment (Figure 1). However, severe herbivory on the plots after their initial green-up limited these efforts. Only one species, *Centarea melitensis*, was unaffected by the herbivory (Figure 2). We hypothesized that its heavily defended exterior was responsible for its survival, not any phenology traits. We did a post hoc analysis on the raw abundance data of *C. melitensis* from SMER to see the effects of treatment and year. The response (slope) of *C. melitensis* was not significantly different between years but treatment was significant for both years and its abundance was positively correlated with increasing watering treatment (Table 2 and Figure 2).

Predictive power of phenology traits

Community weighted trait means of season begin, end, and peak were unaffected by treatment or year in the SMER experimental plots (Table 3). Flowering duration on the other hand, was different between years with a TreatmentxYear interaction (Table 3). There was no difference in community weighted season duration between treatments towards the end of the drought (2016) however community weighted season duration was longest on severe drought plots following drought (2017) (Table 4 and Figure 3).

We ran a follow up analysis to determine whether species origin (highly correlated with life history in this system) interacted with bloom duration. There was not a significant difference in unweighted species bloom duration means between exotic (M=4.9, SD=2.92) and native (M=4.0, SD=1.41) species; t(13)=0.85, p= 0.41 (Figure 4). However, when we calculated weighted bloom duration means by community origin (native and exotic) on severe drought and ambient precipitation plots, there was an origin effect, but not a treatment effect, with exotic species community weighted bloom duration significantly longer on severe drought plots (Table 6 and Figure 5). Native species community weighted means we not affected by origin or treatment.

Ecosystem level phenology

The NDVI on herbaceous dominated open plots was more variable than that of the shrub understory plots (Table 6 and Figure 6). The peak dates for the open herbaceous plots were significantly different between treatments (Table 6) with the productivity peak on severe drought plots being significantly delayed compared to the moderate drought and ambient precipitation treatments. NDVI on severe drought plots was lower than in ambient rainfall plots at the beginning of the season, but higher than in ambient rainfall plots at the end of the season (Figure 6).

NDVI peak dates were significantly later on severe drought plots than ambient precipitation plots in the recovery year (Table 7 and Figure 7). NDVI peak dates were not significantly correlated with community weighted means for bloom duration at the plot level (Cor.coeff =0.08).

Discussion

Previous work in this system showed that the relative abundance of exotic and annual species shifted in response to drought and responded differentially than native and perennial species. Our results monitoring recovery following a four-year drought treatment experiment show that drought combined with previous species shifts (Puritty et al. 2019) produce lasting lagged effects on ecosystem phenology and community weighted phenology traits in a southern California Mediterranean ecosystem. Our findings suggest that the effects of drought in concert with differential responses from native predominately perennial species compared to exotic mostly annual species accentuate the changes in ecological function particularly phenologically. These findings support previous studies showing that drought can can impact ecosystem level phenology by having a multi-year legacy on shifting community composition, particularly within annual dominated areas.

This study shows that seemingly subtle community composition shifts impact overall ecosystem functioning and that the sensitivity of open herbaceous ecosystems to drought disturbance doesn't end once ambient precipitation returns. During drought, the only phenological shift detected by NDVI was a trend for shrub understory plots to extend the length of their growing season (Esch et al in prep) whereas our results show that in the recovery from drought it's the open herbaceous plots rebounding from the most severe drought that exhibited the phenology shift. Previous studies in this system have shown that invasive dominance can happen because of their earlier phenology as compared to natives, not a real competitive ability issue (Puritty et al. 2018) but phenology issue pertaining to priority effects (Cleland et al. 2015). We found a total shift towards later ecosystem phenology when a system is disturbed by the worst drought ever recorded. This response can either re-set the system by allowing for natives to rebound since the early season exotics were so suppressed or it can create a multi-year persistent delayed phenology. In this system the complexity of the response from a mixed cover system is most apparent on a temporal scale in the differential responses to and recovery from drought disturbance.

Species level phenology

Our species level phenology experiment showed that the selected species varied considerably in their peak biomass timing when grown in monocultures. In a long term study of species level phenology in a Mediterranean system, Gordo and Sanz (Gordo and Sanz 2009) found that the growing season phenology shifted earlier for most species but later for other species emphasizing the variation in species level response to disturbances. Our initial results mirrored this pattern of variation until the herbivory events occurred. Esch et al (in revision) found that the presence of exotic species on open herbaceous dominated plots delayed the growing season at the ecosystem level as compared to shrub cover plots, an interesting result given that one of the leading hypotheses for the success of their exotic grasses is their earlier phenology (Wainwright et al. 2012). However, our site is home to two later active exotic species, *Centaurea melitensis* which was documented in this study but also *Hirschfeldia incana*. These species both have large taproots (Moroney et al. 2013; Parsons et al. 2001) which, combined with the increased bare ground and decreased competition on severe drought plots, would allow them to perform even better on drought plots as compared to ambient. As a results, they would be able to deposit more seeds into the seedbank during the drought so that when ambient conditions returned, these forms with later flowering phenology would have a competitive edge on the plots with a history of severe drought. This would support findings that exotic species can evolve in as few as 5 seasons in reaction to drought in Southern

California (Nguyen et al. 2016). We observed much higher cover of both of these species towards the end of the season when the rest of the ecosystem was starting to senesce and they are most likely driving the later community level flowering phenology.

While it was the exotic grass species that drove the initial biomass recovery from drought on open herbaceous plots (Puritty et al. 2019), it was the increases in later season species which drove the community level flowering phenology shift. These results also brought it to our attention that future experiments should include the influence of herbivory on native exotic species interactions as they may be disproportionally influence by herbivore pressure (Waterton and Cleland 2016) and herbivory in the field plays a potentially larger role in ecosystem processes that may not be captured by greenhouse experiments.

Predictive power of phenology traits

The abundance of species with longer community level seasonal flowering duration increased on severe drought open herbaceous plots during recovery from drought. There was no effect of the beginning or end timing of the season because only species with earlier and later seasonal cues benefitted from drought treatments. Our results show that its traits, rather than community level species dissimilarities, that drive this response. This again stresses the differences of shrub understory versus open herbaceous vegetation. Esch et al (in revision) and Bernal et al (2011) showed that Mediterranean shrubs have earlier ecosystem phenology. However long term studies in Mediterranean systems provide evidence that growing seasons were lengthened by 18 days in the US and Europe following drought (Gordo and Sanz 2009; Peñuelas and Filella 2001) which is more in agreement with our findings that species most likely to re-establish after drought had longer seasons. These results have implications for those interested in restoration efforts in this system.

Our findings suggest that seeding areas with native species with longer growing seasons that can persist through severe droughts and be abundant enough to be around to compete with surviving exotic species in the recovery from drought may be one way to cull exotic species spread. This is important because our previous study in this system showed that although exotic biomass dramatically decreases during drought, its ability to recover and rebound to abundances higher than pre-drought conditions poses a potent ecological threat. This dynamic resurgence of exotic biomass has the potential to out compete rare species and when senesced, can increase the fuel load for fires in the dry season. These results point to the potential for improving restoration success by considering community-level flowering phenology.

Ecosystem level phenology

Although exotic species with late duration increased on severe drought plots, our ecosystem measure of peak NDVI was not correlated with our community weighted mean for bloom duration. The unexplained delay in ecosystem phenology could be due to low replication in the experiment, physiological or plastic responses. Alternatively, data from this sight suggests that increased nitrogen deposition on open herbaceous plots under the severe drought treatment could extend the growing season on these plots without a significant shift in species composition.

Native shrub dominated plots did not show any differences in productivity or phenology in their recovery from drought however open herbaceous exotic dominated plots showed later green up and later senescence on the plots that experienced the most severe drought. Previous studies have found that because Mediterranean systems are acclimated to climate fluctuations (Larcher 2000; Peñuelas and Filella 2001) the higher proportion of drought tolerant species lowers the impact of drought (Ciais et al. 2005; Peñuelas et al. 2007). Ivits et al (2014) showed that Mediterranean sites in Europe had stable or longer growing seasons in response to drought. Jentsch et al (2009) were the first to report shifts in phenology as a response to extreme weather events (i.e. drought) in central Europe. They found that only 32 days of drought had the power to shift peak flowering dates 4 days earlier while also extending flowering length 4 days. However, studies focused on Mediterranean plants suggest that drought or drier conditions are more likely to delay flowering phenology (Llorens and Penuelas 2005; Peñuelas et al. 2004). Particularly for drought sensitive shrub species (Ogaya and Peñuelas 2003).

In addition to delayed phenology, Penuelas et al (2004) found that drought extended the flower life span and length of the flowering period of two coastal Mediterranean shrubs. The shrub cover plots followed this predicted pattern in their ecosystem level phenology during drought (Esch et al in prep) but following drought neither the productivity nor the phenology was shifted by previous precipitation variation. However, our finding that open herbaceous dominated plots exhibited delayed phenology in their recovery from drought emphasizes the potential for legacy effects of drought that may not be apparent during the drought. In a previous study, we showed that reductions and resistance of herbaceous plants in the shrub understory during drought is often offset by rapid recovery of herbaceous plant biomass in the open plots following drought (Puritty et al. 2019). Shrubs tend to have earlier ecosystem level seasonal growth in response to drought (Bernal et al. 2011; Prieto et al. 2009) but open herbaceous dominated plots in our study showed later community level flowering phenology following drought. This result contributes to literature stressing the complexity of systems with mixed vegetation (House et al. 2003; Scanlon et al. 2005). Our results support findings from Rich et al. (2008) in that they show differential responses to disturbances of woody versus herbaceous vegetation in productivity but also in phenology.

Conclusion

In conclusion, our findings suggest that the effects of severe drought on community level processes of phenology are not limited to the response to drought but vastly impact the recovery of the ecosystem. Environmental shifts due to drought favored different plant communities and left a signature on the recovery period as well. In our system, severe drought selected for communities with species with that have longer flowering phenology. Although such species may be better equipped to survive in variable years, the impact of this phenological shift on other ecosystems functions in this system are likely to be variable. Our findings suggest that lagged effects of drought on ecosystem function during recovery in conjunction with effects during drought are integral to predicting how mixed Mediterranean ecosystems will be effect by anticipated climate variability.

Chapter 3, in part is currently being prepared for submission for publication of the material. Puritty, Chandler E.; Esch, Ellen H.; Cleland, Elsa E.; Lipson, David A.; The dissertation author was the primary investigator and author of this material.

Tables

Table 3.1. Target species from SMER utilized in the experiment, including origin, life history, flowering phenology traits and growth habit. * denotes species grown in monocultures at BFS to identify species specific phenologies while † identifies the most abundant species at SMER who's abundances were used to calculate community weighted trait means.

taxa	Origin	Life	bloom peak	Bloom duration	Bloom Start	Bloom End	Growth Habit
Anagallis.arvensis †	Exotic	Annual	9	7	6	12	Forb
Bromus.diandrus †	Exotic	Annual	8	3	7	9	Graminoid
*Bromus.hordeaceus** †	Exotic	Annual	7.5	2	7	8	Graminoid
*Bromus.madritensis** †	Exotic	Annual	5.5	2	5	6	Graminoid
Calochortus.splendens †	Native	Perennial	8	3	7	9	Forb
Calystegia.macrostegia †	Native	Perennial	7.5	6	5	10	Forb
*Centaurea.melitensis** †	Exotic	Annual	9	5	7	11	Forb
Cirsium.spp †	Native	Perennial	9	3	8	10	Forb
*Daucus.pusillus** †	Native	Annual	8	3	7	9	Forb
*Dichelostemma.capitatum** †	Native	Perennial	6	3	5	7	Forb
Eriogonum.faciculatum †	Native	Perennial	9.5	6	7	12	Shrub
Erodium.cicutarium †	Exotic	Annual	7	5	5	9	Forb
*Festuca.myuros** †	Exotic	Annual	6.5	4	5	8	Graminoid
Hazardia.squarosa †	Native	Perennial	8.6	5	9	1	Shrub
*Helianthus.gracielentus**	Native	Perennial	10	5	8	12	Forb
Hirschfeldia.incana	Exotic	Perennial	6.5	12	4	3	Forb
Hypochaeris.spp †	Exotic	Annual	7.5	4	6	9	Forb
Lactuca.serriola †	Exotic	Annual	10	5	8	12	Forb
*Salvia.mellifera**	Native	Perennial	8	5	6	10	Shrub
*Stipa.lepida**	Native	Perennial	7	3	6	8	Graminoid
*Stipa.pulchra** †	Native	Perennial	7	3	6	8	Graminoid

BFS monoculture species

†Dominant cover species

Table 3.2. Summary of the effect of drought treatment and year (2016 drought, 2017 recovery) on *C. melitensis* field abundances at SMER.

	χ^2	Df	P-value
Treatment	6.78	1	0.009
Year	0.69	1	0.405
Treatment:Year	0.015	1	0.901

Table 3.3. Summary of the effect of year and treatment on community weighted flowering phenology trait means (duration, peak, begin, end) at SMER experiment on all treatments and both years (2016 drought, 2017 recovery).

		χ^2	Df	P-value
Duration	Treatment	3.18	1	0.07
	Year	8.38	1	0.004
	Treatment:Year	6.54	1	0.011
Peak	Treatment	0.28	1	0.60
	Year	1.54	1	0.21
	Treatment:Year	0.02	1	0.89
Begin	Treatment	0.95	1	0.33
	Year	0.12	1	0.73
	Treatment:Year	0.61	1	0.43
End	Treatment	0.73	1	0.39
	Year	0.38	1	0.54
	Treatment:Year	0.61	1	0.43

Table 3.4. Summary of the effect of year on community weighted flowering phenology duration means across all treatments.

	χ^2	Df	P-value
2016	5.00E-04	1	0.981
2017	7.9082	1	0.0049

Table 3.5. Summary of the interactive effect of drought treatment (severe drought and ambient precipitation only) and origin (native or exotic) on community bloom duration means weighted separately for exotic and native communities at SMER in the recovery year (2017).

	χ^2	Df	P-value
Treatment	1.97	1	0.16
Origin	15.95	1	<0.001
Treatment:Origin	2.84	1	0.09

Table 3.6. Summary of the effect of community composition (shrub cover or open herbaceous) and drought treatments on productivity as measured by NDVI for each time point in a single growing season (2017 recovery).

		χ^2	Df	P-value
4-Jan	Treatment	11.1	1	<0.001
	CC	1.49	1	0.22
	Treatment:CC	7.78	1	0.005
26-Jan	Treatment	1.09	1	0.29
	CC	2.54	1	0.11
	Treatment:CC	5.33	1	0.02
9-Feb	Treatment	0.22	1	0.63
	CC	2.59	1	0.11
	Treatment:CC	1.46	1	0.23
23-Feb	Treatment	0.75	1	0.38
	CC	1.88	1	0.16
	Treatment:CC	0.43	1	0.51
8-Mar	Treatment	0.0002	1	0.99
	CC	3.96	1	0.046
	Treatment:CC	0.11	1	0.73
24-Mar	Treatment	2.53	1	0.11
	CC	2.43	1	0.12
	Treatment:CC	0.28	1	0.59
5-Apr	Treatment	6.21	1	0.013
	CC	0.091	1	0.76
	Treatment:CC	0.11	1	0.74
16-Apr	Treatment	5.23	1	0.022
	CC	6.86	1	0.009
	Treatment:CC	0.33	1	0.56
28-Apr	Treatment	5.64	1	0.018
	CC	11.6	1	<0.001
	Treatment:CC	0.40	1	0.52
14-May	Treatment	4.10	1	0.043
	CC	28.4	1	<0.001
	Treatment:CC	0.47	1	0.49
27-May	Treatment	3.83	1	0.05.
	CC	51.6	1	<0.001
	Treatment:CC	0.37	1	0.54

Table 3.7. Summary of the effect of treatment, community weighted bloom duration means, and any interactions on plot level date at peak NDVI at SMER in the recovery year.

	χ^2	Df	P-value
CWM duration	2.70	1	0.10
Treatment	7.88	1	0.01
CWM duration::Treatment	0.01	1	0.93

Figures

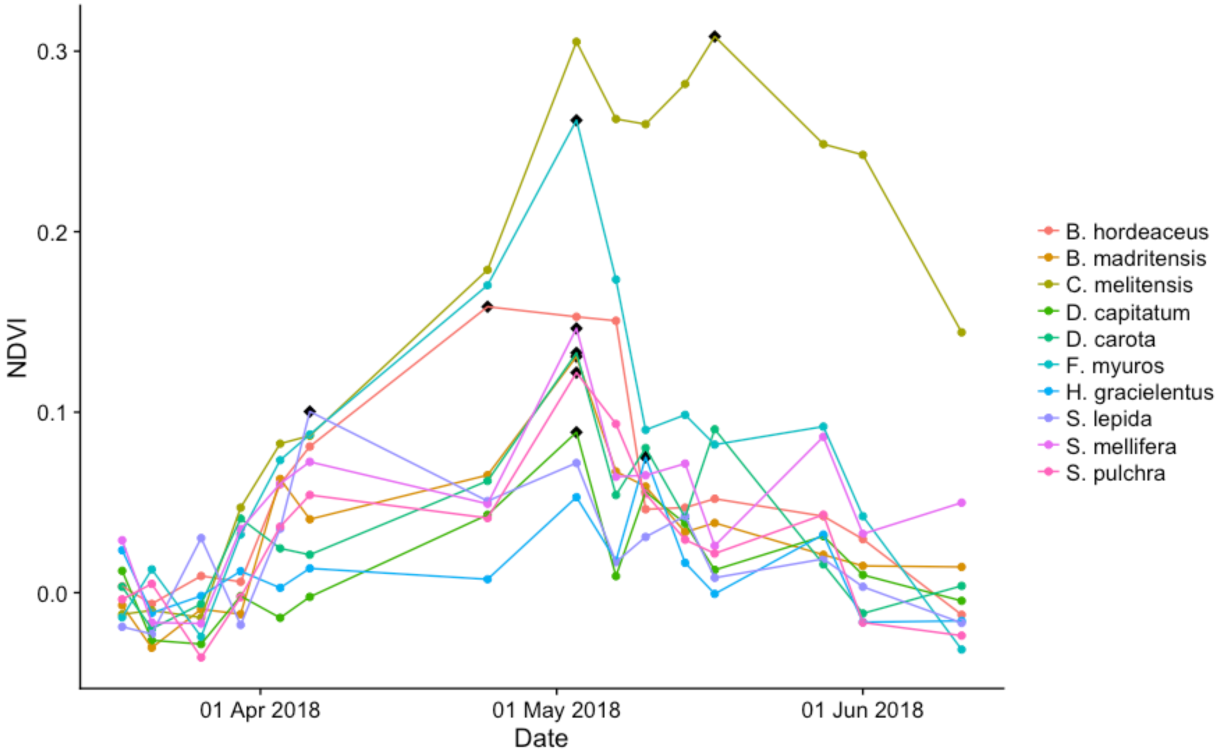

Figure 3.1. NDVI on each measurement date for each of the 10 species grown in monocultures in a single season. Colors correspond to species and the black diamonds represent the peak NDVI for each species.

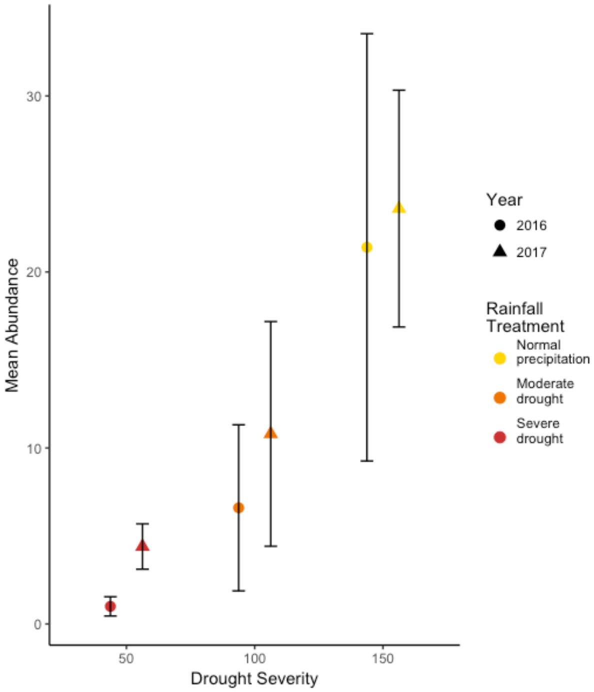

Figure 3.2. Mean abundance of *C. melitensis* as shown by percent cover in the field at SMER across all drought treatments and over two years (2016 drought, 2017 recovery). Color corresponds to drought treatment while shape corresponds to year.

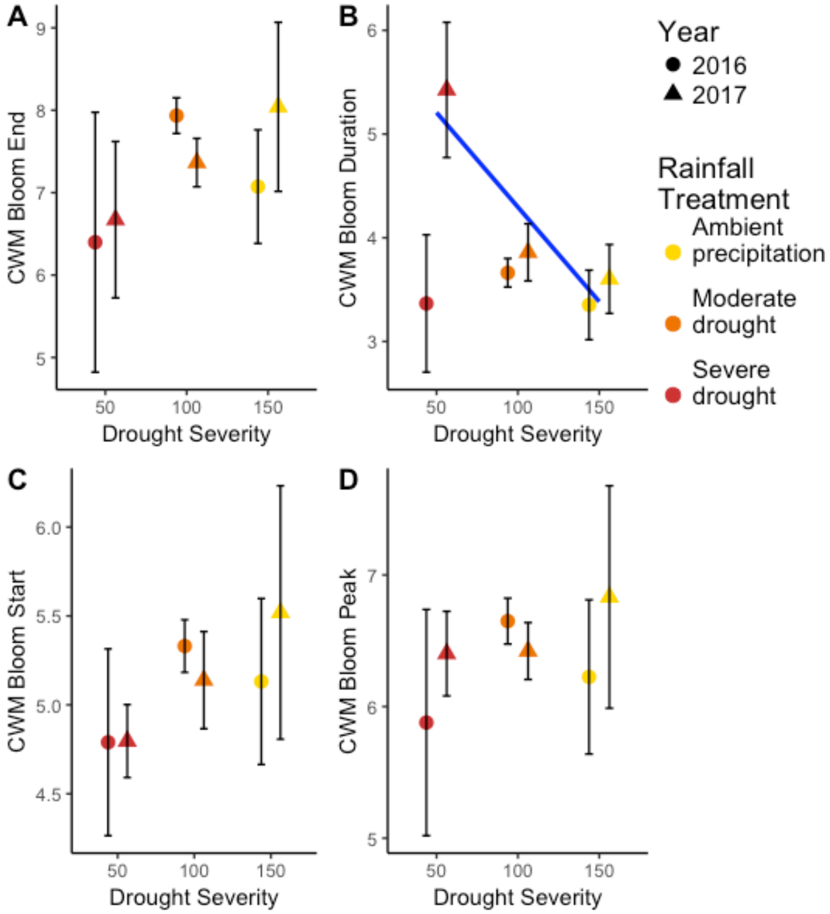

Figure 3.3. Community weighted flowering phenology trait means for (a) end, (b) duration, (c) start, and (d) peak across all drought treatments over two years (2016 drought, 2017 recovery). Color corresponds to drought treatment while shape corresponds to year.

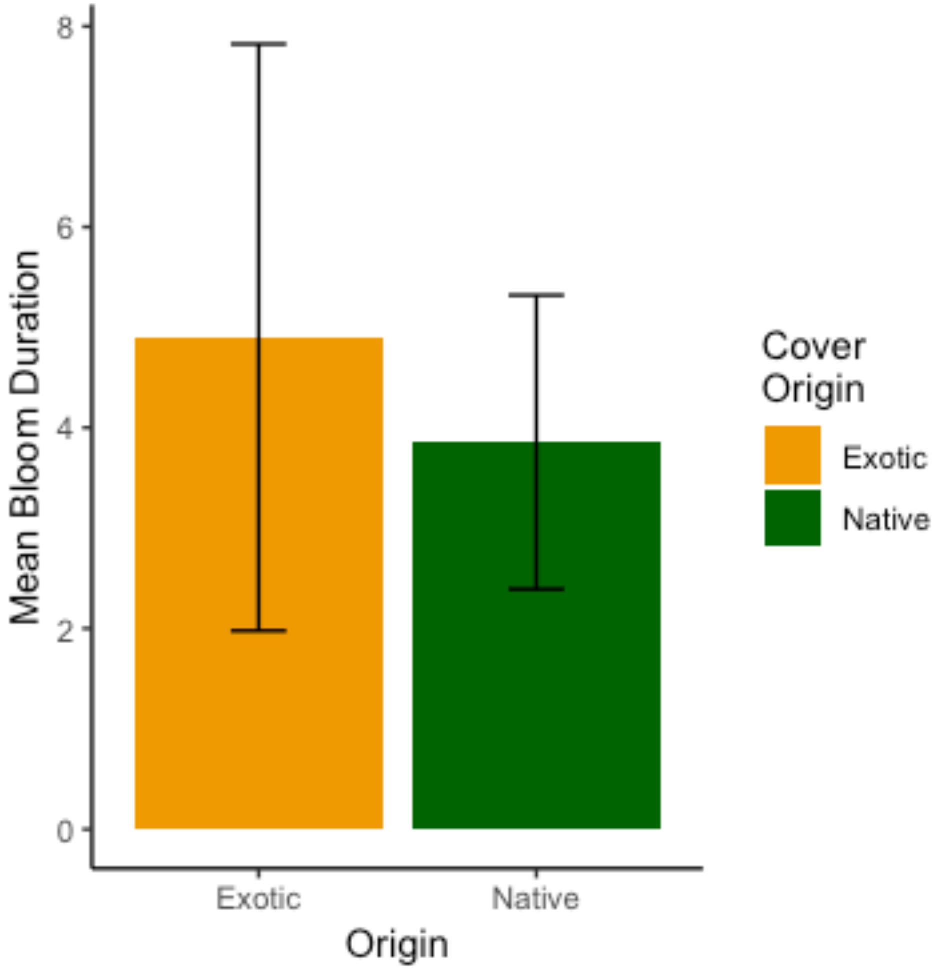

Figure 3.4. Unweighted bloom duration trait means for native (green) and exotic (gold) species. Color corresponds to origin.

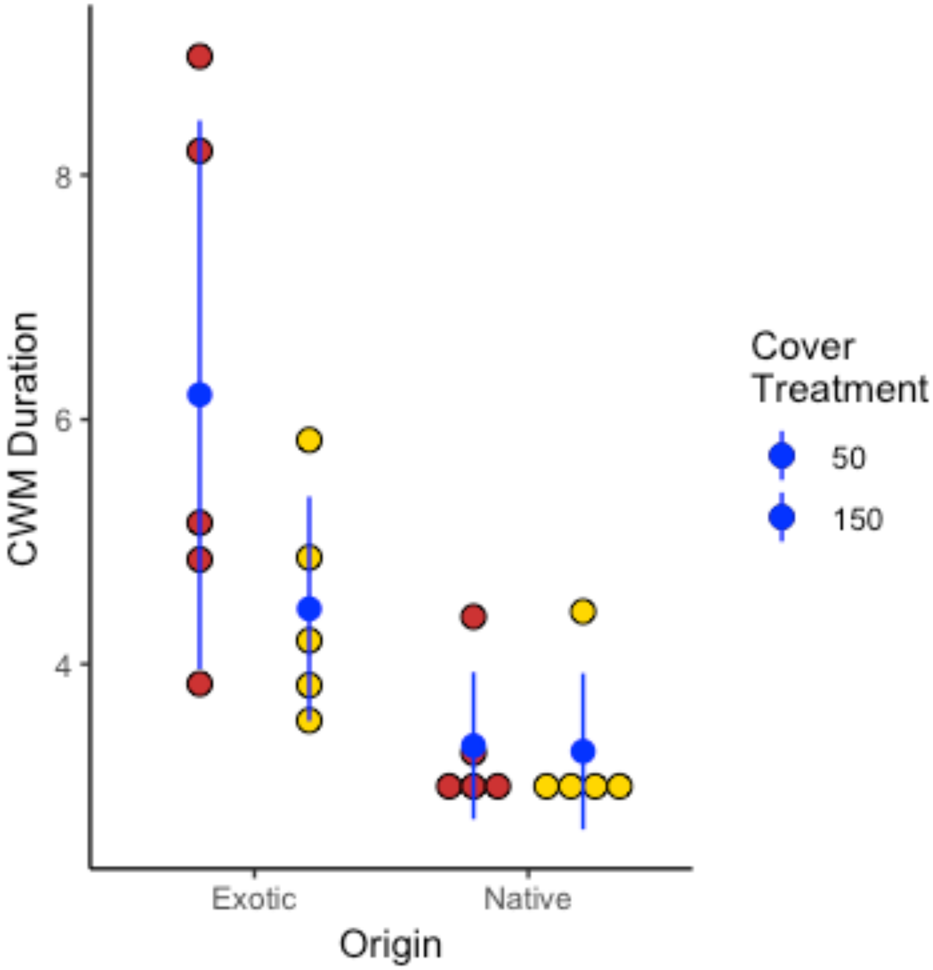

Figure 3.5. Community bloom duration means weighted separately for exotic and native communities on severe drought and ambient precipitation plots during the recovery year (2017). Color corresponds to treatment.

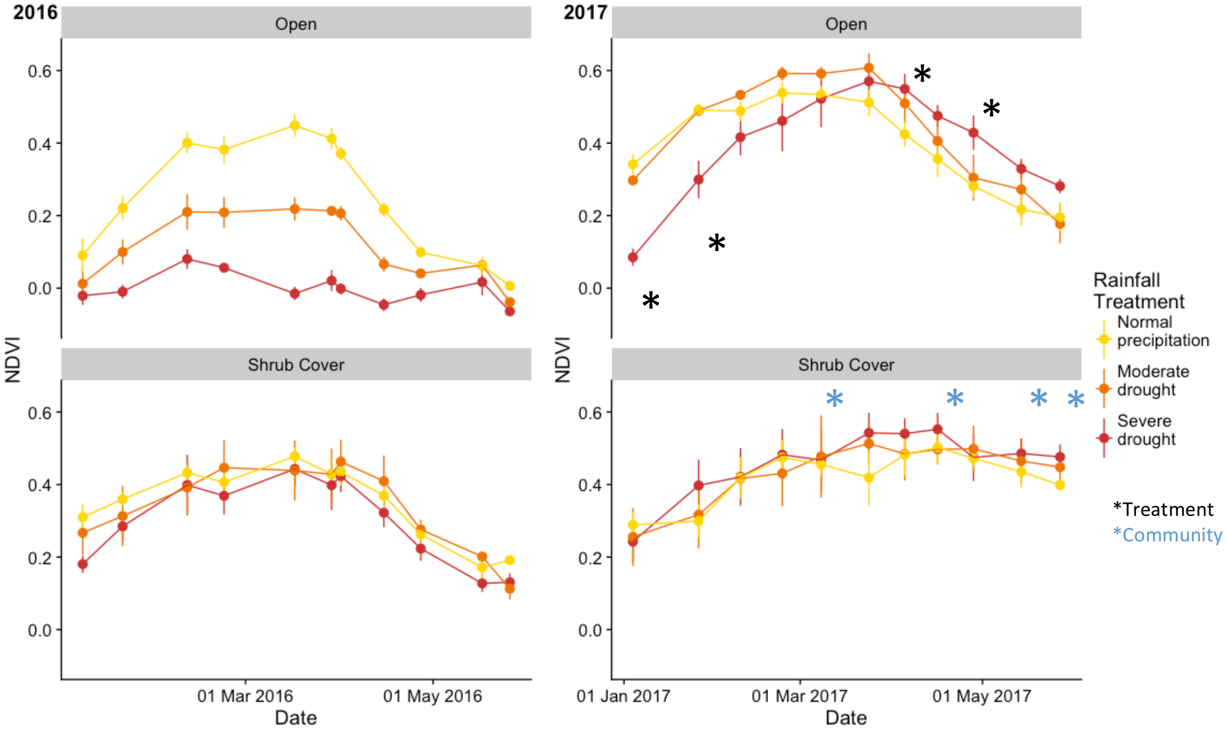

Figure 3.6. NDVI on each measurement date for open plots dominated by herbaceous species, and shrub cover plots, during drought (2016) and recovery (2017). Colors indicate experimental rainfall treatments (red = severe drought, orange = moderate drought, yellow = ambient precipitation), and error bars represent ± 1 SE. Blue stars indicate where NDVI differs between communities while black stars show differences between treatments.

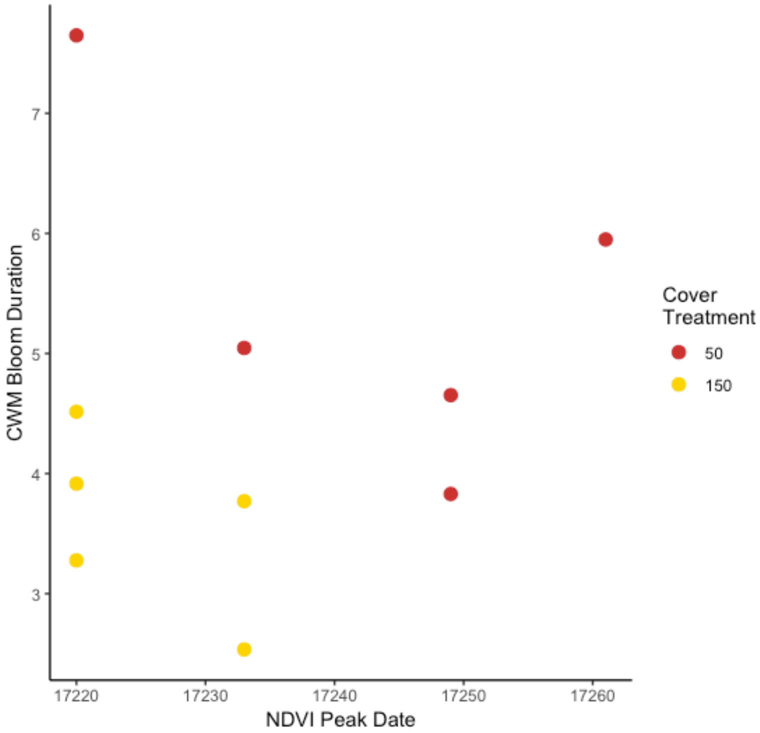

Figure 3.7. NDVI peak date plotted against community weighted bloom duration means. Color corresponds to treatment.

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Conclusion

Global climate change and invasion have a number of influences on ecosystem functioning. However, how the magnitude and duration of their combined impact on ecosystems is less clear. This dissertation set out to ask how invasion influences ecosystem response to and recovery from drought. First, functional traits were the best predictor of competitive outcomes between native species and a common invasive grass. In accordance with limiting similarity, the communities that are most resistant to invasion are those with resource-acquisition and seedling phenology traits similar to the invader whereas communities with species whos traits differ are most susceptible under ambient precipitation conditions. Second, under precipitation variation the community assembles according to the life history differences between the predominately perennial native community and the majority annual exotic community in a natural system. While native biomass was more resistant to change during drought, the precipitation pulse in the recovery from drought causes a major increase in the proportion of annual species which are largely exotic and can increase fire frequency. Third, a legacy of severe drought increased the proportion of species with long bloom duration at a community level and triggered delayed phenology at the ecosystem level in the first year of recovery. This major shift in community assembly around bloom duration was driven by an exotic perennial species. The effect on plot phenology as a measure of ecosystem functioning was more difficult to predict and could be due to shifts in community assembly selecting for a higher proportion of later active exotic species or to physiological/trait plasticity. In sum, my dissertation suggests that invasion coupled with an increase in inter-annual precipitation variation changes community assembly. Under ambient conditions, the community assembles according to differences in resource-acquisition traits;

under drought conditions, it assembles according to life history; and under high precipitation conditions (recovery), it assembles according to duration of flowering phenology. There is also evidence of invasion and precipitation variation shifting ecosystem functioning to later phenology although because it could not be correlated with flowering phenology, the mechanism remains unknown. Invaded semi-arid and arid ecosystems are at high risk of species loss and a state shift towards exotic dominated grassland communities in response to inter-annual precipitation variation.