UC Riverside

UC Riverside Electronic Theses and Dissertations

Title

Understanding Mechanisms of Invasion Dynamics and Their Associated Impacts on Native Species in Dryland Plant Communities

Permalink

https://escholarship.org/uc/item/2xh4n202

Author

Rodriguez, Clarissa

Publication Date

2023

Copyright Information

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

RIVERSIDE

Understanding Mechanisms of Invasion Dynamics and Their Associated Impacts on
Native Species in Dryland Plant Communities

A Dissertation submitted in partial satisfaction

of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Clarissa Rodriguez

September 2023

Dissertation Committee:
Dr. Loralee Larios, Chairperson
Dr. Janet Franklin
Dr. Erin Wilson-Rankin

The Dissertation of Clarissa Rodriguez is approved:

_____

_____

_____

Committee Chairperson

University of California, Riverside

ABSTRACT OF THE DISSERTATION

**Understanding Mechanisms of Invasion Dynamics and Their Associated Impacts on
Native Species in Dryland Plant Communities**

by

Clarissa Rodriguez

Doctor of Philosophy, Graduate Program in Botany & Plant Sciences
University of California, Riverside, September 2023
Dr. Loralee Larios, Chairperson

An ongoing critical challenge in invasion ecology is the ability to predict invader responses to environmental change and their associated impacts on native resident communities, especially in historically uninvaded systems such as North American drylands. Biological invasions occur over distinct stages such as introduction (i.e., species introduced into novel ranges), establishment (i.e., species establishing self-sustaining populations), and spread (i.e., species dispersing and expanding their ranges), and different factors may mediate invasion dynamics within each of these stages. Thus, I designed my dissertation to focus on identifying the drivers and impacts of invasive species establishment and spread, as well as investigating effective strategies to manage biological invasions in temporally variable environments. My dissertation uses a combination of observational, experimental, and modeling-based approaches to elucidate the mechanisms that allow invaders to establish, spread and persist in dryland systems. Chapter 1– spread – assessed the role of environmental niche shifts in facilitating the spread of a winter annual invasive plant, *Brassica tournefortii* (sahara mustard) in North

America. Through a biogeographic approach, I discovered that despite having a relatively unchanged and consistent environmental niche (including climate and soil conditions), *Brassica tournefortii* still has a significant amount of available and unused habitat in its introduced North American range. These findings indicate that the invader may persist in spreading throughout North America and highlight potential regions where preventative measures can be taken. Chapter 2 – impact – leveraged a long-term dataset to understand how attributes of an invasion regime influence community synchrony and stability in a stabilized sand dune system. I found that both boom frequency and the dominant magnitude of invader boom are strong predictors of community synchrony and stability, becoming more asynchronous and less stable as the intensity of invasion increases. Further, the underlying invasion level mediates the dynamics that a system experiences. These findings move beyond basic invader abundance-native diversity metrics and shed light on additional factors that may be contributing to invader impacts in these historically uninvaded environments. Chapter 3 – management – addressed the role of seasonality during herbicide applications for the control of an emerging invasive winter annual forb, *Oncosiphon pilulifer* (stinknet). I found that seasonal herbicide efficacy is contingent on the density of invasive species stored within the soil seed bank, highlighting the importance of incorporating above and below-ground metrics of community composition when evaluating strategies for invasive plant management. For instance, in areas that have a long history of invasion (i.e., saturated invader seed bank), using pre-emergent herbicides provides higher control compared to post-emergent herbicide. These findings allowed me to make recommendations to land practitioners on

when to apply herbicides to limit the spread of invasive species. Overall, the results from

my dissertation provide insight into the mechanisms that allow invasive species to spread

and persist within historically uninvaded landscapes.

TABLE OF CONTENTS

CHAPTER 3 Efficacy of invasive plant control depends on season of herbicide application and invader soil seedbank density

GENERAL INTRODUCTION

The field of ecology continues to place a strong emphasis on the study of biological invasions due to the variety of impacts invasive species have on ecosystems, such as their ability to alter community structure, biogeochemistry, or disturbance regimes (Elton, 1958; Ricciardi et al. 2013; Roy et al. 2023). Within the field of invasion ecology, we recognize biological invasion to occur as a process over four distinct stages (i.e., transport, introduction, establishment and spread), with their own barriers that non-native species must overcome to reach the status of "invasive" (Blackburn et al. 2014). The barriers that species must overcome encompass concepts derived from various sub-disciplines of ecology, such as geographical and dispersal barriers (i.e., biogeography and landscape ecology), as well as survivorship and establishment barriers (i.e., community and population ecology), providing insight into how some species become invasive while others fail to overcome barriers (Shea & Chesson, 2002; Wolkovitch & Cleland, 2015; Vila & Ibanez, 2011). Historically, at the population and community level, invasion ecology has focused on understanding how invaders can establish and persist in a community by identifying traits of successful invaders and characteristics that make communities invasible (Londsdale, 1999; Stachowicz and Tilman, 2005). Despite these efforts, a critical challenge in invasion ecology continues to be the ability to predict invader responses to environmental change, and impacts exerted on resident communities, especially in historically uninvaded systems. Since biological invasions

occur over a series of stages, several dynamics may develop over time, further complicating the ability to assess drivers and impacts of invasive species on plant communities.

Predicting the spread of invasive species is a crucial aspect of invasion ecology, especially with the ongoing influx of introduced species and the expansion of already-established invaders (Seebens et al. 2017). Accurate predictions can help in developing management strategies to mitigate invader spread and prevent further impacts. These predictions of invader spread are often based on two concepts: 1) climate matching and 2) niche conservatism. The climate matching hypothesis states that habitats that encompass climate similar to that of the invader's native range will be more susceptible to invader spread (Broennimann et al. 2008), and niche conservatism asserts that the niche of a species remains unchanged over time (i.e., niche stability) (Ackerly, 2003). Together, these concepts have been applied towards creating species distribution models to predict the spread of invaders (Jeschke & Strayer 2008; Mainali et al. 2015). Undoubtedly, climate is an important factor for predicting the spread of species; however, these modeling efforts often overlook the possibility for niche expansion (i.e., the ability for a species to adapt to its new environment and expand its breadth of environmental tolerances) as a mechanism of invasion. Failure to account for this mechanism, or other differences in the realized niches between native and introduced ranges can lead to underestimation of suitable habitat predictions within the introduced range, resulting in further spread of the species than predicted (Ackerly, 2003; Atwater et al. 2018). Mis-predicting the spread of invasive species can further exacerbate the ecological and

economic costs associated with invasive species management. For instance, misleading predictions about invader spread can result in the misallocation of limited resources and cause harm to resident species in invaded regions that were incorrectly identified as areas with low risk of spread (Battini et al. 2019). Therefore, identifying how the realized environmental niches of an invasive species' native and introduced range overlap may be important in enhancing our ability to make predictions of invader spread under future climate conditions.

Identifying the full distributional range of an invader can contribute towards prioritizing invasive species management and improved tracking of invader abundance and their subsequent impacts. Evaluating impacts of invaders on recipient communities has been a fundamental focus in ecology (Parker et al. 1999; Richardson & Pysek, 2008), concentrating on invader abundance as a key driver of community impacts (Bradley et al. 2019). However, in communities that experience cyclical dynamics, such as boom-bust cycles, tracking invader impacts by invader abundance alone may be more challenging due to temporal fluctuations in species abundances (Strayer et al. 2017). For instance, in temporally variable environments, environmental fluctuations can elicit differential responses from species, due to differences in species traits (e.g., germination cues and seed banking strategies), that allow for species to circumvent or mediate competition and maintain species diversity (Angert et al. 2009; Gremer et al. 2016). This diversity in species life history strategies is important for maintaining the stability of ecosystem functioning over time as it can result in species asynchrony with different species being

able to dominate in different conditions (Zhang et al. 2022). In these temporally dynamic systems, its critical to evaluate community responses to invaders over longer time scales (Crystal-Ornelas & Lockwood, 2020).

When evaluating invader impacts in cyclical systems, it is crucial to understand the fluctuating patterns of invader abundance over time. Frequency and magnitude of invader booms, for example, may mediate the impacts of invasion on recipient ecosystems. Communities that experience more frequent invader booms may result in more degraded communities due to dynamics that accumulate and carryover to future years, such as high seed production that is stored in a seedbank (Giora et al. 2014). Thus, monitoring an invader boom's frequency and magnitude over time and time between booms can potentially reveal which aspects of the invasion regime harm the resident community and result in altered communities. Therefore, in systems that experience cyclical dynamics, it is necessary to evaluate temporal dynamics of both the invader and the recipient community to fully understand the impact that invaders have on communities.

Despite much research being done on various approaches to managing invasive species, community and ecosystem responses to management strategies remain highly variable due to invader impacts that lead to native recovery constraints, such as altered soil biota, soil nutrient cycling or propagule pools (Levine et al. 2003; Carr et al. 2019; Hess et al. 2019; Funk et al. 2020). Altered propagule pools in particular are a key factor facilitating the dominance of non-native invasive species while limiting the recovery of native species (Larios et al. 2013). Conducting more holistic assessments of potential

propagule sources at a site can help provide initial insights to post-management

trajectories. When evaluating a seedbank, it's important to take note of the types of

propagules present. If the majority of the propagules are non-native species, it indicates a

higher risk of secondary invasion. On the other hand, if the native species are dominant, it

suggests that passive recovery may occur. Notably, seedbanks can be a critical repository

for seeds and can mediate plant community composition after disturbances in systems

with variable climate (Chesson 2000, Angert et al. 2009), yet the role of seedbanks are

often overlooked when assessing invader management strategies.

When considering that herbicides are one of the most commonly utilized

strategies to control invasive plants, evaluating the responses of the focal invader above

and belowground is important to be able to assess the full potential for a management

strategy to control the spread of an invader. For instance, invasive species may produce

enough propagules to saturate the soil seedbank with seeds, potentially influencing future

recruitment events even after management efforts have been applied (Schwartz-Lazaro &

Copes, 2019). Additionally, the long-term presence of an invader at a site can deplete the

seedbank of native species, further reducing the potential for native species recruitment

post-management (Robertson & Hickman, 2012). In areas with variable climate, such as

California, many native annual species have long-lived seeds in the soil seedbank that

may not be represented in the aboveground vegetation at a given time, highlighting the

importance of conducting management assessments both above and belowground, over

multiple growing seasons to capture interannual variation in plant communities (LaForgia

et al. 2018). Further, implementing invasive plant control efforts with a limited

understanding of unintended management outcomes, can hinder meeting other management goals (i.e., increasing native diversity), at the expense of reducing invasive plant abundance (Kettenring & Adams 2011).

To gain a better understanding of these potential outcomes, it is imperative to carefully consider temporal dynamics that may mediate the effectiveness of invasive plant strategies. For example, when evaluating chemical management options, assessing temporal dynamics such as how the seasonal timing of herbicide applications (i.e., fall vs spring), and how often herbicide applications are required to successfully control the focal invader populations are important to consider, as these factors may mediate the effectiveness of long-term invasive plant management, especially in highly variable environments. Understanding the temporal dynamics is therefore essential for interpreting the variability in community responses to different invasive plant management strategies. Having this knowledge is critical in developing effective management strategies that can achieve multiple objectives in restoration efforts. Thus, evaluating management strategies can be strengthened by assessing both above and belowground communities over several growing seasons, helping us gain a better understanding of when and how to manage invasive species.

Thus, the goal of my dissertation is to assess how a variety of ecological drivers influence invasion dynamics to improve predictions of invader response to environmental change and impacts on communities. Specifically, I ask: 1) How can we predict the spread of invaders? 2) How are invaders impacting the recipient community? and 3) How can we effectively manage invasive species?

6

Study System: North American drylands provide a model system to investigate plant invasion dynamics. These ecosystems are characterized by high interannual variability and contain a diversity of native annual plants (Schwinning & Sala, 2004; Barrows et al. 2009; Gill et al. 2018). Over the past century, global warming has substantially impacted drylands, with models forecasting an additional 2-4°C increase by the end of this century (Huang et al. 2017). Furthermore, climate models project the Southwestern United States to increase in variability of annual and seasonal precipitation (Seager et al. 2007; Zhang et al. 2021). Changes in precipitation regimes can lead to drastic effects on ecosystems since water is the primary environmental limiting factor in drylands (Sala et al. 2012). Further, dryland systems have historically been considered to be resistant to invasion due to the stressful nature of the environment; however, within the past few decades ecologists have recognized the ability of certain non-native plants to tolerate the harsh conditions and establish viable populations in these communities leading to changes in ecosystem structure and function (Brooks, 1999; Baez et al. 2008). Therefore, investigating how species respond to environmental fluctuations and temporal change within drylands is of utmost importance to predict future invasion success under continued climate change.

References.

Ackerly DD (2003) Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. International Journal of Plant Sciences 164:S165–S184

Angert AL, Huxman TE, Chesson P, Venable DL (2009) Functional tradeoffs determine species coexistence via the storage effect. Proceedings of the National Academy of Sciences of the United States of America 106:11641–11645

Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nature Ecology & Evolution 2:34–43

Báez S, Collins SL (2008) Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. PloS One 3:e2332

Barrows CW, Allen EB, Brooks ML, Allen MF (2009) Effects of an invasive plant on a desert sand dune landscape. Biological Invasions 11:673–686

Battini N, Farías N, Giachetti CB, Schwindt E, Bortolus A (2019) Staying ahead of invaders: using species distribution modeling to predict alien species' potential niche shifts. Marine Ecology Progress Series 612:127–140

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology 12:e1001850

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26:333–339

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019a) Disentangling the abundance-impact relationship for invasive species. Proceedings of the National Academy of Sciences of the United States of America 116:9919–9924

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019b) Disentangling the abundance–impact relationship for invasive species. Proceedings of the National Academy of Sciences 116:9919–9924

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters 4:585–589

Brooks ML (1999) Habitat invasibility and dominance by alien annual plants in the western Mojave Desert. Biological Invasions 1:325–337

Carr AN, Hooper DU, Dukes JS (2019) Long-term propagule pressure overwhelms initial community determination of invader success. Ecosphere 10-e02826

Charles H, Dukes JS (2008) Impacts of Invasive Species on Ecosystem Services. In: Biological Invasions. Ecological Studies Springer, Berlin, Heidelberg pp. 217–237.

Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366

Crystal-Ornelas R, Lockwood JL (2020) The 'known unknowns' of invasive species impact measurement. Biological Invasions 22:1513–1525

Elton CS The Ecology of Invasions by Animals and Plants. Methuen, London.

Funk JL, Parker IM, Matzek V, Flory SL, Aschehoug ET, D'Antonio CM, Dawson W, Thomson DM, Valliere J (2020) Keys to enhancing the value of invasion ecology research for management. Biological Invasions 22:2431–2445

Gill RA, O'Connor RC, Rhodes A, Bishop TBB, Laughlin DC, St Clair SB (2018) Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall. Oecologia 187:755–765

Gioria M, Jarošík V, Pyšek P (2014) Impact of invasions by alien plants on soil seed bank communities: emerging patterns. Perspectives in Plant Ecology, Evolution and Systematics 16:132-142.

Gremer JR, Kimball S, Venable DL (2016) Within-and among-year germination in Sonoran Desert winter annuals: bet hedging and predictive germination in a variable environment. Ecology Letters 19:1209-1218

Hess MCM, Mesléard F, Buisson E (2019) Priority effects: Emerging principles for invasive plant species management. Ecological Engineering 127:48–57

Huang J, Li Y, Fu C, Chen F, Fu Q, Dai A, Shinoda M, Ma Z, Guo W, Li Z, Zhang L, Liu Y, Yu H, He Y, Xie Y, Guan X, Ji M, Lin L, Wang S, Yan H, Wang G (2017) Dryland climate change: Recent progress and challenges. Reviews of Geophysics 55:719–778

Jeschke JM, Strayer DL (2008) Usefulness of bioclimatic models for studying climate change and invasive species. Annals of the New York Academy of Sciences 1134:1–24

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. The Journal of Applied Ecology 48:970–979

LaForgia ML, Spasojevic MJ, Case EJ, Latimer AM, Harrison SP (2018) Seed banks of native forbs, but not exotic grasses, increase during extreme drought. Ecology 99:896–903

Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B 270:775–781

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Mainali KP, Warren DL, Dhileepan K, McConnachie A, Strathie L, Hassan G, Karki D, Shrestha BB, Parmesan C (2015) Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. Global Change Biology 21:4464–4480

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999b) Impact: Toward a Framework for Understanding the Ecological Effects of Invaders. Biological Invasions 1:3–19

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83:263–282

Richardson DM, Pyšek P (2008) Fifty years of Invasion Ecology - the legacy of Charles Elton. Diversity & distributions 14:161–168

Robertson SG, Hickman KR (2012) Aboveground plant community and seed bank composition along an invasion gradient. Plant Ecology 213:1461–1475

Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Sankaran, K. V., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., and Vandvik, V (2023) Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany.

Sala OE, Gherardi LA, Reichmann L, Jobbágy E, Peters D (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philosophical transactions of the Royal Society of London. Series B, Biological Sciences 367:3135–3144

Schwartz-Lazaro LM, Copes JT (2019) A Review of the Soil Seedbank from a Weed Scientists Perspective. Agronomy 9:369

Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8:14435

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

Stachowicz JJ, Tilman D (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. Species Invasions: Insights into Ecology, Evolution, and Biogeography 41–64

Strayer DL, D'Antonio CM, Essl F, Fowler MS, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pyšek P, Robertson P, von Schmalensee M, Stefansson RA, Wright J, Jeschke JM (2017) Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecology Letters 20:1337–1350

Vilà M, Ibáñez I (2011) Plant invasions in the landscape. Landscape Ecology 26:461–472

Wolkovich EM, Cleland EE (2014) Phenological niches and the future of invaded ecosystems with climate change. AoB Plants 6: 2041–2851

Zhang Z, Hautier Y, Bao T, Yang J, Qing H, Liu Z, Wang M, Li T, Yan M, Zhang G (2022) Species richness and asynchrony maintain the stability of primary productivity against seasonal climatic variability. Frontiers in Plant Science 13:1014049

Chapter 1

High potential for *Brassica tournefortii* spread in North American introduced range,

despite highly conserved niche

Abstract: Identifying areas vulnerable to the spread of invasive species is critical for designing effective management plans. Species distribution modeling is commonly used to predict species suitable habitat. However, invasive species may not be in equilibrium with environmental conditions within the introduced range, leading to inaccurate predictions. We focused on *Brassica tournefortii* to (1) assess the role of niche dynamics, (2) identify environmental drivers facilitating spread, and (3) identify suitable habitat within currently un-invaded areas in North America (introduced range) by quantifying the realized niche in its home range (Mediterranean basin and Middle East) and introduced range. *Brassica tournefortii* continues to expand its distribution within North America, threatening native species and altering ecosystem dynamics through invasion. We found that *Brassica tournefortii* has a highly conserved environmental niche, driven primarily by warm and dry climates with resource-limited soils. Despite high niche stability, we detected environmental non-equilibrium between the ranges, with 55% niche unfilling and 1% expansion into more arid and resource-limited environments within the introduced range. Our distribution models also highlighted invadable regions in the introduced range where this species is not found currently, indicating opportunities for this species to continue to spread within North America, and suggesting that previous

estimates may underestimate areas at risk for invasion. To improve spatial predictions of

the potential spread of invasive species, we must consider the role that niche dynamics

and environmental equilibrium play during biological invasions.

Introduction. Identifying areas at risk for the potential spread of invasive species is essential for prioritizing invader management and prevention efforts to reduce an invader's ecological impacts. Species distribution modeling (SDM) is one important tool that can forecast invader spread by creating spatial predictions of species suitable habitat and identifying important drivers of species distributions (Franklin, 2010). However, when species are introduced to novel areas, a variety of niche dynamics can emerge depending on whether the introduced area matches or differs from the environmental conditions of a species' native range (Broennimann et al. 2012; Atwater et al 2018). A species' niche may be consistent between the native and introduced ranges (i.e., niche conservatism or stability), or a species niche may experience a shift to match environmental conditions in its introduced range. Many studies often assume this and fail to account for potential niche shifts within the introduced range. Failure to account for niche shifts can lead to underestimating suitable habitat within the introduced range, limiting our ability to predict invader spread and successfully manage invaders (Pili et al. 2020).

Evidence for niche shift dynamics between species' native and introduced ranges is equivocal. Some studies support that niche shifts are rare (Petitpierre et al. 2012) and focus on dynamics of how a species occupies similar niche space between the native and introduced range. Within this niche conservatism approach, a species may exhibit a suite of potential dynamics (Fig. 1): 1) where they occupy the same suitable habitat in both ranges (i.e., stability), 2) where they fail to occupy suitable habitat in the introduced range that is occupied in the native range (i.e., unfilling) or 3) where they are occupying

suitable habitat in the introduced range that is not occupied in the native range (i.e.,

expansion) (Atwater et al 2018). Unfilling is important for predicting the spread of

species since these conditions are considered suitable for the species but are unoccupied,

perhaps due to limitations in dispersal or lag effects in spread (Qiao et al. 2017).

Moreover, niche unfilling may occur among species that are not in equilibrium with their

environment (i.e., species-environment non-equilibrium). Expansion, conversely, can be

due to changes in biotic pressures (i.e., enemy release hypothesis), physiological

adaptations, or high phenotypic plasticity of the invader in the introduced range (Atwater

et al. 2018). Conversely, other studies support that niche shifts are relatively common

among invasive species (Atwater et al. 2018), showing that in models comparing the

climatic niche of species' native and introduced ranges, shifts are often dependent on the

species growth forms and traits (Wang & Wan, 2021; Vásquez-Valderrama et al. 2022).

When the underlying niche conservatism and species-environment equilibrium

assumptions are violated, this can lead to underestimating the spread of invasive species

and reduced spatial transferability (Mainali et al. 2015; Andrade et al. 2019, Liu et al.

2022), thus limiting the applicability of SDMs for invasive species management.

With this in mind, researchers have emphasized that the approach used to model

invasive species distributions matters and should be standardized to include the native

and introduced ranges to facilitate comparisons between studies and improve spatial

predictions (Broennimann & Guisan 2008; Guisan et al. 2014; Di Cola et al. 2017). Yet,

spatial predictions for invasive species continue to rely on data from the introduced range

only (Kariyawasam et al. 2019; Jarnevich et al. 2022). For species that are continuously

spreading and have broad distributional ranges, using a subset of available data for model training may result in inaccurate model predictions (Yates et al. 2018), particularly if the niche conservatism or species-environment assumptions are violated (Foster et al. 2022). Hence, the importance of incorporating occurrence data from the native and introduced ranges when modeling distributions of invasive species.

Our ability to detect shifts is improved when we expand beyond models that only use climatic predictors. Edaphic factors such as soil texture and nutrient availability (Ulrich et al. 2014; Maestre et al. 2021) are also major factors related to plant distributions and can contribute valuable information as to what is driving the establishment and spread of a species but are not regularly included in SDMs. In one study, Velazco et al. (2017) found that distribution models that included both edaphic and climatic variables as predictors improved model accuracy compared to models that only included climatic predictors. Additionally, defining the species fundamental niche (i.e., full range of environmental conditions a species can theoretically live in) is often unfeasible, emphasizing the importance of studying niche shifts within analogous environments in order to capture changes within the realized niche (e.g., environmental conditions that a species currently occupies). Disentangling dynamics comparing non-analogous environments is challenging with only information on the species occupied (realized) niche. Capturing broader species-environment relationships beyond climate may help further delimit invasive species establishment and spread patterns.

Brassica tournefortii (Brassicaceae; sahara mustard) is an herbaceous winter-annual forb native to the Mediterranean basin and parts of the Middle East. This species

was accidentally introduced into North America through California's date palm tree trade in 1920 (Minnich and Sanders 2000). Despite the early introduction year, this species has only more recently (within the past 2-3 decades) started rapidly expanding across southwestern United States and Northern Mexico, altering ecosystem dynamics in the process (Winkler et al. 2018). This invader reduces native plant flowering and fruiting within the Colorado desert by 80-90% in sand dune communities, threatening many endemic plants (Barrows et al. 2009). Additionally, *Brassica tournefortii* has been linked to changes in community structure by reducing plant and arthropod richness and abundance within drylands (Van Tassel et al. 2014). With the distribution of this species continuing to spread, efforts to model spread are critical to help invasive plant management minimize any further impacts.

Species distribution models have been developed to understand the drivers of *Brassica tournefortii's* spread and improve the management of this species. However, those models have either been limited to regional scales (Berry et al 2016; Sanchez-Flores, 2007), have primarily focused on climatic factors (Curtis and Bradley, 2015), and all except Li et al (2015) have used occurrence points from only the introduced range of the species to calibrate their models. Additionally, this species can adjust certain physiological traits such as phenology and investment in reproductive structures to match environmental drivers in the North American introduced range (Marushia et al. 2010; Winkler et al. 2018), making it an exceptional study system to test the niche conservatism and species-environment relationships that are important to modeling invasive plant species distributions.

Here, we use a global biogeographic approach to assess the potential spread of *Brassica tournefortii* in its North American introduced range. We first assess underlying niche dynamics and ask 1) Is *B. tournefortii's* environmental niche conserved within its North American introduced range? and 2) What climatic and edaphic factors are shaping the distribution of *B. tournefortii*'s environmental niche within its introduced range? Lastly, we forecast invasion potential and ask 3) What un-invaded areas within the North American introduced range support suitable habitat for *B. tournefortii*? Answering these questions will provide a more holistic understanding of the variables driving the spread of the species and improve the accuracy of spatial predictions to be used for invasive species management.

Methods. Species Records. We retrieved 12,620 global occurrence records in both *Brassica tournefortii's* native range and North American introduced range using four databases: Global Biodiversity Information Facility (GBIF.org, DOI10.15468/dl.4fmk2n), SEInet (biodiversity data accessed through Data Portal, http//:swbiodiversity.org/index.php, 2022-03-14), Integrated Digitized Biocollections (https://www.idigbio.org/portal, 2016) and research-grade occurrence points from iNaturalist (DOI10.15468/dl.wbw2pe) from 1950-2022. Occurrence data were cleaned using the 'bdc' package in R (Ribeiro et al 2022) by georeferencing records, removing duplicates, adding a geographic correction filter to remove records within 3 km of capital city and province/state centroids, records within 10 km around country centroids, records within 111 km of the GBIF headquarter, records within 100 m of zoo and herbaria to exclude cultivated occurrences, and lastly applied a 0.1 distance in decimal degrees

buffer around the country records for coordinate precision. After the filters were applied, we identified 8,138 unique occurrence points (native range = 517; introduced = 7,620).

Environmental Variables. To assess the factors shaping the distribution of *B. tournefortii*, we focused on environmental variables that are important drivers of plant community dynamics in drylands, where this species commonly invades (Williams et al. 2012). Since this species is an annual winter forb (germinating in response to cold-season precipitation), bioclimatic variables were selected to capture intra-annual seasonality and annual average temperature and precipitation during the winter growing season (Table 1). We also selected edaphic variables important to plant establishment and growth dynamics. Bioclimatic factors averaged from 1950-2000 were downloaded at a 1 km spatial resolution from the WorldClim database, version 2.1 (Hijmans et al. 2005), and the edaphic variables were retrieved from the ISRIC World Soil Information database at a 250 m resolution (Poggio et al. 2021). Since predictors varied in resolution, we used a bilinear interpolation method, which calculated a weighted average of nearby cells to resample the original soil layers to create a common resolution of 1 km. We performed a correlation analysis among bioclimatic and edaphic variables to detect pairs with a high correlation >|0.75|, resulting in 12 uncorrelated predictor variables. These included six bioclimatic variables and six edaphic variables (Table 1).

Data Analysis: Niche dynamics. To assess the role of niche dynamics in facilitating the spread of *B. tournefortii* in North America, we first limited the model training areas and study extent to the World Wildlife Fund's terrestrial ecoregions (Olson et al. 2001) found within the native range of the species and containing occurrence data (Table 2). These

included 1) temperate conifer forests, 2) temperate grasslands, savannas, and shrublands, 3) Mediterranean forests, woodlands, and scrub, and 4) deserts and xeric shrublands (Fig. 2). To quantify the environmental niche of the native and North American introduced ranges that are within the ecoregions found in the native area, we used the Centroid shift, Overlap, Unfilling, and Expansion (COUE) methodological framework (Broennimann et al. 2012) in the 'ecospat' package in R (Di Cola et al. 2017). To assess the contribution of our 12 variables to the environmental niche, we ran a Principal Component Analysis (PCA), and created a density distribution for each grid cell using a kernel density function for the native range environmental niche and the introduced range environmental niche. We then used the first two axes of the PCA to quantify niche overlap between the two ranges by using Schoener's D metric (Schoener, 1968), which compares native and introduced range density distributions, calculating a number ranging between 0 and 1, where 1 indicates complete niche overlap. To test if the niche is conserved, we ran niche similarity and equivalence tests comparing the overlap between the native and North American introduced niches to 1000 randomly generated null distributions (Warren et al. 2008). We then quantified the following niche dynamics between the two ranges in analogous environmental space: niche stability, niche unfilling, and niche expansion.

Data Analysis: Species distribution modeling. To identify areas vulnerable to the spread of *Brassica tournefortii* within the introduced range, we used an ensemble SDM approach that combines predictions of various modeling techniques to reduce model uncertainty (Araújo et al. 2007; Thuiller et al. 2019). We used the same 12 environmental

variables and study extent used to analyze niche dynamics to create our SDMs. To reduce

sampling bias and redundancy in environmental space, which can influence model

prediction, we used environmental filtering to thin the original 8,138 occurrence records

to 1,843 records used for modeling (Varela et al. 2014; Velazco et al. 2020). We used an

environmental filtering procedure in which occurrence records are filtered based on

partitions or bins in environmental space, where more bins result in a greater number of

filtered occurrence records. Because environmental filtering is sensitive to the number of

bins (i.e., number of classes in which each environmental variable is split) used to divide

environmental space, we tested 2, 3, 4, 6, 8, and 12 bins and then calculated the resulting

spatial autocorrelation between variables based on the Moran's I index. The number of

bins with the lowest average spatial autocorrelation between variables and the highest

number of occurrences (12) was selected to filter occurrence records. Twelve bins was

the optimal split. We therefore split the environmental variables into 12 groups and

filtered species occurrences based on their environmental conditions, resulting in 1,843

records.

To measure model transferability, models were evaluated regarding their capacity

to project on geographical areas different from those used for model training (Roberts et

al. 2017). We applied a spatial block partitioning method by partitioning our data into 12

spatially structured groups. To select the block cell size that best fit our species records,

we tested 30 sizes (range of block size resolution). The optimum grid size was the one

with the lowest spatial autocorrelation (i.e., Moran's I), maximum environmental

similarity (i.e., minimum Euclidean distance), and the minimum difference of records

among groups (i.e., standard deviation-SD; Velazco et al., 2019) based on our data set. Since our dataset consists of presence-only records, which is often the case for introduced species, we generated pseudo-absence records equivalent to the number of presence-only records to be able to use species distribution modeling techniques that require presence-absence data. Additionally, we created 18,000 background points (required by MAXENT) throughout the extent of our study area and extracted environmental variable data from our presence/pseudo-absence and background data before fitting our models.

We implemented five commonly used SDM algorithms: Generalized Linear Model (GLM), General Boosted Regression Model (GBM), Support Vector Machine Model (SVM), Random Forest model (RFM), and Maximum Entropy (MAXENT). For all our models, we obtained suitability values using the threshold that maximized the Sorensen similarity index, where values above the threshold were designated as suitable habitat, while values below this threshold were designated as non-suitable habitat. We fitted the GLM using a binomial distribution family and second-degree polynomials for continuous variables. For MAXENT, we used cloglog transformations as the response type. To optimize the performance of our algorithms, we performed hyperparameter tuning for GBM, SVM, RFM, and MAXENT algorithms with a range of specific values for our species (see supplemental table 1. for model tuning and hyperparameter values), where the Sorensen metric was used for selecting the best combination of hyperparameters to tune each model (Schratz et al. 2019).

To further increase model transferability and reduce model uncertainty, we created ensemble models using the predictions of individual models with an AUC >0.95

(indicating high accuracy). GBM, SVM, RFM and MAXENT models were all retained to create an ensemble model, using the same threshold and performance metrics used for fitting and validating the individual models. We tested three types of ensemble modeling approaches - 1) using a weighted average based on model performance (meanw) (based on the Sorensen index), 2) using the average of the best models (meansup) (average of the models with above average performance according to Sorensen index), and 3) averaging cells with suitability values above the threshold that maximized the Sorensen index (meanth) - and selected the best performing ensemble model (meanw). Using the output of the ensemble model, we created a geographical prediction of habitat suitability across our focal species' study extent. All SDMs were created using the 'flexsdm' package in R (Velazco et al. 2022). We performed all analyses using R version 4.1.2. (R Core Team, 2021).

Results.

Niche dynamics

We found low niche overlap (*Schoener's D* = 0.25, where 0 indicates no overlap and 1 represents complete overlap) between the native and introduced range of *Brassica tournefortii*. When we compared the niche overlap to null distributions, we found that the niches were not identical (niche equivalence test, p=0.009) between ranges, but the similarity (overlap) was greater than expected by chance (niche similarity test, p=0.005), indicating evidence for niche conservatism (Fig. 3A; SI. Fig. 1). We found additional support for niche conservatism when we assessed individual niche dynamics and found

that 99% of the occupied niche in the introduced range is stable (i.e., falls within the

native range niche; gray shading in Fig. 3A). This suggests that although niche overlap is

low between ranges, this is primarily due to unfilling, not expansion; this species

occupies very similar environments in both ranges. We additionally observed that this

species occupied similar environmental space in both ranges, as most occurrences existed

within environmental space that is relatively common between both ranges (Fig. 3B-C).

Our models also detected extensive suitable environmental conditions available within

the introduced range (Fig. 3C) that remain unoccupied, primarily within environmental

conditions that are relatively rare within the native range (Fig. 3B). The differences

between commonality of environmental densities (depicted by green pixels in Fig. 3B-C)

between ranges explain the overall low niche overlap value. Specifically, we found that

55% of this species' environmental niche remains unfilled within the introduced range,

revealing evidence for species-environment non-equilibrium. We did identify a small

(1%) niche expansion within the introduced range, indicating the *B. tournefortii* is

occupying some areas with environmental conditions that had not been previously

occupied within the native range.

Drivers of Distribution

We found that the twelve predictor variables selected for this study explained

70.37% of the variation in our data, with the first PCA axis explaining 50.45% and the

second PCA axis explaining 19.92% (Fig. 3D). The first PCA axis (PC1) described a

gradient of soil structure and soil water availability, where negative values were

associated with greater available water holding capacity, higher percent silt, clay and low

bulk density, while positive values had higher bulk density and percent sand. The second

PCA axis (PC2) described a gradient of precipitation and temperature, where negative

values were associated with cold-wet winters, and warm summers, while positive values

had higher seasonal temperature ranges and precipitation variation. Further, our

ordination revealed that soil variables along PC1 (Fig. 3D) are the main drivers of

variation within the native environmental density (Fig. 3B). In contrast, within the

introduced range, temperature, and precipitation variables along PC2 strongly influence

environmental density (Fig. 3C) in addition to soil variables.

Within *Brassica tournefortii's* stable environmental niche, we found that species

occurrence density coincided with the warmest temperatures of the coldest quarter (i.e.,

winter), and the driest quarter (i.e., summer), suggesting this species prefers to establish

in warm conditions (Fig. 3D). We also found that this species is not strongly influenced

by interannual variability in precipitation as the contribution of precipitation seasonality

to the current stable range was relatively weak, indicated by the blue arrow in Fig. 3D,

compared to the other predictor variables. In addition to arid climate, we also found that

this species is mainly found on soils that have high bulk density and sand content, as well

as low resource availability (e.g., low soil organic carbon, available water holding

capacity).

Most niche unfilling occurred in environments that contained relatively cooler

and wetter climate during the growing season, as well as soils with higher nutrient

content compared to the stable niche (Fig 3D). Yet, we also detected a portion of niche

unfilling within environments that had even more arid climate and sandier soil than areas

25

currently occupied within the introduced range. We also observed drivers of niche

expansion and found that this species is expanding its realized niche within the

introduced range into more arid environments with higher seasonal variations in

temperatures compared to environments occupied within the native range.

Habitat Suitability

Our SDMs performed very well across the different algorithms, with AUC values

ranging from 0.97-0.98 (Table 3). Ensemble models that used a weighted average based

on model performance had the highest model performance compared to the other

ensemble modeling approaches and was used to create spatial predictions (AUC: $0.988 \pm$

0.003, TSS: 0.92 ± 0.02, Boyce Index: 0.97 ± 0.019, Sorensen: 0.963 ± 0.01, for all model

performance see supplemental Table. S1.)

Based on our ensemble model, we found contrasting distributions of habitat

suitability between native and introduced ecoregions (Fig 4). In the native range, we

observed that most of the highly suitable habitat (within the range of 0.70-1; blue to

purple colors) was found in the Mediterranean ecoregion. Despite the desert and xeric

shrubland ecoregion comprising a large portion of the native range, most habitat found

within this ecoregion was predicted to have low suitability (0-0.50). However, our models

did identify moderate (0.50-70) to high habitat suitability within countries in the middle

east near the Mediterranean and Arabian sea, suggesting that this species mainly occupies

coastal rather than inland habitat within the native range. As for the temperate grasslands

and temperate conifer forests within the native range, our models predicted low to no

habitat suitability within these ecoregions.

Like the native range, Mediterranean forests, woodlands, and scrub ecoregions also contained highly suitable habitat in the introduced range. In contrast to this species' native distribution patterns, we found that desert and xeric ecoregions within the introduced range contained the largest amount of highly suitable habitat and occurrences (Table 2). Similar to our findings of stable and expansion niche dynamic drivers, we found that high habitat suitability was primarily found in warm and dry environments with resource-limited soils. For instance, "warm" deserts such as the Chihuahuan, Sonoran and Mojave deserts contained the highest suitability, reflecting current invasion patterns for *Brassica tournefortii* within North America. The Great Basin Desert, conversely, which is considered a "cool" desert, had either no or very low habitat suitability, demonstrating that the spread of this species is likely limited by cold winter temperatures during its growing season. Our models also detected suitable habitat within North American temperate conifer forests and temperate grasslands, where this species is currently not found. However, suitability was low (<0.5) and limited in extent, likely due to these ecoregions containing more productive soils and cooler and wetter environments.

Discussion. Comparing the realized environmental niche between a species' native and introduced range is critical to improving predictions of invader spread. Here, we build on previous modeling efforts of habitat suitability for *Brassica tournefortii* by comparing the realized environmental niches between native and introduced ranges and expanding the environmental niche dimensions to include edaphic as well as climatic factors to understand the full breadth of environmental tolerances of the species. Our study provides support for the role of edaphic variables such as soil structure and soil properties

in influencing the distribution of *B. tournefortii,* in addition to the limited edaphic and topographic variables previously identified for this species (Sanchez-Flores, 2007; Berry et al. 2016). In our study, using a biogeographic approach revealed that despite having a highly conserved and stable environmental niche (very little niche expansion), *B. tournefortii* is not at equilibrium with its environment within the introduced range, as it still has substantial unfilled habitat remaining. This suggests that our focal invader is not restricted to resource-limited drylands in its introduced range and has the potential to continue to spread into both more mesic and more extreme xeric habitats within the unoccupied but suitable habitat in North America.

Evaluating niche shift dynamics is key to better estimating suitable habitat and mechanisms of spread within introduced ranges (Broenimann & Guisan, 2008; Guisan et al. 2014). Failure to account for niche conservatism can often result in inaccurate predictions of niche shifts when indeed a species is demonstrating niche unfilling (Petittpierre et al. 2012). In our study, we observed that *B. tournefortii* exhibited strong niche unfilling, and these findings are consistent with previous studies that have found that niche unfilling is more common than niche expansion among introduced species (Strubbe et al. 2013; de Andrade et al 2019; Liu et al 2020). However, we did observe small evidence of niche expansion where the invader was expanding into environments that were hotter and drier compared to its native range. Petittpierre et al. (2012) previously identified a similar pattern of niche expansion for species that are native to Europe and introduced to Australia and North America. However, due to the limited occurrence records of *B. tournefortii* in its native range compared to the availability of

records within the introduced range in our study, there is a possibility that the 1% niche expansion we observed is an artifact of sampling bias. Moreover, with the disparity in sampling efforts across the globe, we encourage the implementation of international BioBlitz to increase data acquisition by academic and community scientists, especially in data-limited geographic regions. Community science efforts are a cost-effective way to both improve species surveillance and build stronger connections between community members, policy makers, and scientists (Cesar de Sa et al. 2019; Roy-Dufresne et al. 2019).

Considering that numerous invasive species can tolerate a broad range of environmental conditions, the accuracy of climate change and range-shifting species distribution models are likely to benefit from using data sets that use a global biogeographic approach to train models and expand beyond climatic predictor variables. For instance, climate change projection models created using regional datasets from the introduced Southwest United States predicted a 34% reduction in *Brassica tournefortii* presence under conservative climate change, and a 29% expansion under worst-case climate change scenarios (Curtis & Bradley, 2015). According to our study, a large portion of the Southwestern United States is already considered suitable habitat under current climate conditions, which was not captured using the regional dataset from the introduced range. Additionally, we observed range-specific drivers of occurrence between the native and introduce ranges; within *B. tournefortii's* native range, factors related to soil structure and soil water availability were the main drivers; while precipitation played a bigger role in driving the species distribution compared to soil properties within the

29

introduced range. Range-specificity can occur among invasive species with large niche breadths as a result of provenance-by-environment interactions, where the evolutionary history in the native range leads to pre-adapted genotypes that can respond in distinct ways depending on the interactions encountered within the new range (Zenni et al. 2014; Eyster & Wolkovich, 2021). As the changing climate continues to alter ecosystems globally, it is important to use a biogeographic approach to capture as much of the environmental tolerance and range-specificity to identify drivers of invasive species spread.

Our study demonstrated that *B. tournefortii's* stable niche includes occurrences that commonly occupy arid and resource-limited environments, reflecting current patterns of invasion by this species in North American drylands, but it is important to note that biotic interactions also play an important role in determining a species' distribution. Our study revealed a large amount of highly suitable, but unoccupied habitat within California's coastal Mediterranean ecoregion. This habitat like much of California's mesic and semi-arid landscapes has a long history of disturbance and invasion, with several taxonomically related invasive mustards (i.e., *B. nigra*, *Hirshchfeldia incana*, *Sisymbrium irio)* already occupying this range. Competition with these other mustards may be hindering *B. tournefortii*'s ability to colonize the unfilled Mediterranean ecoregion) (Marushia et al 2012). Moreover, native species and invaders within this region can promote plant-soil feedbacks that inhibit germination and establishment of other species including taxonomically related mustards such as *B. tournefortii* (Singh & Meyer, 2020; Miller et al. 2021). In the case of temperate conifer forest and grassland ecoregions where

30

our models predicted habitat as low-mid suitability, the combination of dispersal limitations, as well as the vegetation of the resident communities (i.e., trees and shrubs) suggest a low probability of invasion in these areas. In temperate ecoregions, limited light interception through the canopy increases competition among understory species, further influencing herbaceous annual species establishment and growth (Landuyt et al. 2021).

Another compelling facet of interpreting niche dynamics (although outside of the scope of this study) is the potential for increased evolutionary capacity through multiple introductions. In our study, we observed that *Brassica tournefortii* tolerates a broad range of environmental conditions. This may be because there have been at least three separate introductions of *B. tournefortii* in North America from different geographic locations within its native range, resulting in three genetically distinct sub-populations, with evidence of some admixture between populations (Winkler et al. 2018). The multiple introductions of this species into North America may be contributing to increased genetic diversity and phenotypic plasticity, potentially contributing to the broad environmental tolerances. Future studies should focus on testing the evolutionary and physiological differences between the subpopulations of *B. tournefortii* to provide insights into eco-evolutionary dynamics that may be facilitating the spread of this species.

Implementing knowledge about the mechanisms driving niche dynamics can improve the management of biological invasions. Prevention and eradication of invading species are highly plausible if plans for Early Detection and Rapid Response (EDRR) are put into effect in areas identified as containing environmental conditions that match a species niche unfilling or expansion. For instance, despite the high habitat suitability within the

North American Mediterranean ecoregion, *B. tournefortii* has not occupied all suitable

habitat, indicating niche unfilling. In these unfilled areas, *B. tournefortii* should be added

to invasive species watch lists to detect early germinants and prevent the spreading of

populations. In addition to monitoring detection, it is important for management plans to

limit the spread of invasive species is by controlling human-mediated dispersal. Road

networks are a common way for species to hitchhike to new locations, especially for *B.*

tournefortii, which grows abundantly along roadsides in North American deserts (Trader

et al. 2006; Sanchez-Flores, 2007). Increased collaborations between scientists and

stakeholders (i.e., department of transportation services) across multiple states are needed

to effectively plan the maintenance (i.e., timing of mechanical or chemical removal) and

surveillance of currently invaded roadsides (Davies & Sheley, 2007; Otto & Brunson,

2021). Additionally, raising public awareness of invasive species spread through

strategies such as installing hiking trail signage to inform the public on invasive species'

impacts on native communities, organizing community weed management volunteer

days, and encouraging the engagement of the public to participate in BioBlitz may

contribute to reducing human-mediated dispersal (Graham et al. 2018). Accordingly,

minimizing the spread of invaders requires interdisciplinary collaborations and

community support to detect, track and manage invaders.

Our findings highlight the importance of standardizing invasion modeling approaches

to explicitly test and account for underlying assumptions of niche conservatism and

species-environment equilibrium to improve the accuracy of spatial predictions for

invasive species, as well as to be able to compare studies using a similar methodology

(i.e., COUE Framework) to inform the niche shift debate (Catford et al 2022; Guisan et al. 2014). As climate change models continue to forecast increased aridity in North America (Seager et al. 2007; Overpeck & Udall, 2020), it is critical that we identify range-specific drivers of species distribution and identify areas that may be at risk of future invasion within North America. Modeling efforts can be paired with EDRR plans to monitor the leading edge of an invader within the introduced region to limit spread.

References.

Araújo MB, New, Mark (2007) Ensemble forecasting of species distributions. Trends in Ecolohy & Evolution 22:42–47

Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nature Ecology & Evolution 2:34–43

Barrows CW, Allen EB, Brooks ML, Allen MF (2009) Effects of an invasive plant on a desert sand dune landscape. Biological Invasions 11:673–686

Berry KH, Gowan TA, Miller DM, Brooks ML (2014) Models of Invasion and Establishment for African Mustard (Brassica tournefortii). Invasive Plant Science Management 7:599–616.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Toccoz NG, Thuiller W, Fortin MJ, Tandin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21:481–497

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters 4:585–589

Catford JA, Wilson JRU, Pyšek P, Hulme PE, Duncan RP (2022) Addressing context dependence in ecology. Trends in Ecology & Evolution 37:158–170

Curtis CA, Bradley BA (2015) Climate Change May Alter Both Establishment and High Abundance of Red Brome (Bromus rubens) and African Mustard (Brassica tournefortii) in the Semiarid Southwest United States. Invasive Plant Science Management 8:341–352

de Andrade AFA, Velazco SJE, De Marco P (2019) Niche mismatches can impair our ability to predict potential invasions. Biological Invasions 21:3135–3150

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774–787

Eyster HN, Wolkovich EM (2021) Comparisons in the native and introduced ranges reveal little evidence of climatic adaptation in germination traits. Climate Change Ecology 2:100023

Foster SL, Kharouba HM, Smith TW (2022) Testing the assumption of environmental equilibrium in an invasive plant species over a 130 year history. Ecography 12-e12933

Franklin J (2010) Mapping species distributions: spatial inference and prediction

Graham S, Metcalf AL, Gill N, Niemiec R, Moreno C, Back T, Ikutegbe V, Hallstrom L, Ma Z, Lubeck A (2019) Opportunities for better use of collective action theory in research and governance for invasive species management. Conservation Biology 33:275–287

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. Trends in Ecology & Evolution 29:260–269

Hengl T, de Jesus JM, Heuvelink GB, Gonzalez MR, Kilbarda M, Blagotic A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B, Guevara MA, Vargas R, MacMilan RA, Batjes NH, Leenaars JG, Ribeiro E, Wheeler I, Mantel S, Kempen B (2017) SoilGrids250m: Global gridded soil information based on machine learning. PLOS ONE 12:e0169748

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal Climatology 25:1965–1978

Hulton VanTassel HL, Hansen AM, Barrows CW, Latif Q, Simon MW, Anderson KE (2014) Declines in a ground-dwelling arthropod community during an invasion by Sahara mustard (Brassica tournefortii) in aeolian sand habitats. Biol Invasions 16:1675–1687

Kariyawasam CS, Kumar L, Ratnayake SS (2019) Invasive Plant Species Establishment and Range Dynamics in Sri Lanka under Climate Change. Entropy 21 6-571

Li YM, Dlugosch KM, Enquist BJ (2015a) Novel spatial analysis methods reveal scale-dependent spread and infer limiting factors of invasion by Sahara mustard. Ecography 38:311–320

Liu C, Wolter C, Courchamp F, Roura-Pascual N, Jeschke JM (2022) Biological invasions reveal how niche change affects the transferability of species distribution models. Ecology e3719

Maestre FT, Benito BM, Berdugo M, Berdugo M, Concostrina-Zubiri L, Delgado-Baquerizo M, Eldridge DJ, Guirado E, Gross N, Kefi S, Le Bagousse-Pinguet Y, Ochoa-Hueso R, Soliveres S (2021) Biogeography of global drylands. New Phytologist 231:540–558

Marushia RG, Cadotte MW, Holt JS (2010) Phenology as a basis for management of exotic annual plants in desert invasions. Journal of Applied Ecology 47:1290–1299

Miller AD, Inamine H, Buckling A, Roxburgh SH, Shea K (2021) How disturbance history alters invasion success: biotic legacies and regime change. Ecology Letters 24:687–697

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Poweell GV, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC, Loucks CK, Allnutt TF, Ricketts TH, Kura Y, Lamoureaux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51:933–938

Otto N, Brunson M (2021) Cross-boundary weed management in protected area–centered ecosystems: how can it work and what makes it harder to achieve? Invasive Plant Science Management 14:183–189

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348

Pili AN, Tingley R, Sy EY, Diesmos MLL, Diesmos AC (2020) Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Scientific Reports 10:7972

Qiao H, Escobar LE, Peterson AT (2017) Accessible areas in ecological niche comparisons of invasive species: Recognized but still overlooked. Scientific Reports 7:1213

Ribeiro BR, Velazco SJE, Guidoni-Martins K, Tessarolo G, Jardim L, Bachman SP, Loyola R (2022) bdc: A toolkit for standardizing, integrating and cleaning biodiversity data. Methods in Ecology & Evolution 13:1421–1428

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arriota G, Hauensteun S, Lahoz-Monfort JJ, Schroder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929

Sánchez-Flores E (2007) GARP modeling of natural and human factors affecting the potential distribution of the invasives Schismus arabicus and Brassica tournefortii in "El Pinacate y Gran Desierto de Altar" Biosphere Reserve. Ecological Modelling 204:457–474

Sanders A, Minnich R (2000) Brassica tournefortii. Invasive plants of California's wildlands University of California Press, Berkeley, CA

Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418

Schratz P, Muenchow J, Iturritxa E, Richter J, Brenning A (2019) Hyperparameter tuning and performance assessment of statistical and machine-learning algorithms using spatial data. Ecological Modelling 406:109–120

Singh M, Meyer WM (2020) Plant-Soil Feedback Effects on Germination and Growth of Native and Non-Native Species Common across Southern California. Diversity 12:217

Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob Ecol Biogeogr 22:962–970

Suding KN, Stanley Harpole W, Fukami T, Kulmatiski A, MacDougall AS, Stein C, van der Putten WH (2013) Consequences of plant--soil feedbacks in invasion. J Ecol 101:298–308

Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019) Uncertainty in ensembles of global biodiversity scenarios. Nat Commun 10:1446

Trader MR, Brooks ML, Draper JV (2006) Seep Production by the non-native Brassica tournefortii (sahara mustard) along desert roadsides. Madrono 53:313–320

Ulrich W, Soliveres S, Maestre FT Gotelli NJ, Quero JL et al. (2014) Climate and soil attributes determine plant species turnover in global drylands. Journal of Biogeography 41:2307–2319

Varela S, Anderson RP, García-Valdés R, Fernández-González F (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37: 1084-1091

Vásquez-Valderrama M, Carmona CP, Pauchard A (2022) Invasive woody legumes: Climatic range shifts and their relationships to functional traits. Global Ecology & Biogeography 31:2397-2409

Velazco SJE, Galvão F, Villalobos F, De Marco Júnior P (2017) Using worldwide edaphic data to model plant species niches: An assessment at a continental extent. PLoS One 12:e0186025

Velazco SJE, Ribeiro BR, Laureto LMO (2020) Overprediction of species distribution models in conservation planning: A still neglected issue with strong effects. Biological Conservation 252:108822

Velazco, S. J., Rose, M. B., de Andrade, A. F., Minoli, I. & Franklin, J. (2022). flexsdm: An R package for supporting a comprehensive and flexible species distribution modelling workflow. Methods in Ecology and Evolution 13:1661–1669

Wang C-J, Wan J-Z (2021) Functional trait perspective on suitable habitat distribution of invasive plant species at a global scale. Perspectives in Ecology and Conservation 19:475–486

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883

Williams KJ, Belbin L, Austin MP, et al (2012) Which environmental variables should I use in my biodiversity model? International Journal of Geogrpahical Information Science 26:2009–2047

Winkler DE, Gremer JR, Chapin KJ, et al (2018) Rapid alignment of functional trait variation with locality across the invaded range of Sahara mustard (Brassica tournefortii). American Journal of Botany 105:1188–1197

Yates KL, Bouchet PJ, Caley MJ, et al (2018) Outstanding Challenges in the Transferability of Ecological Models. Trends in Ecology & Evolution 33:790–802

Zenni RD, Bailey JK, Simberloff D (2014) Rapid evolution and range expansion of an invasive plant are driven by provenance-environment interactions. Ecology Letters 17:727–735

Figures & Tables.
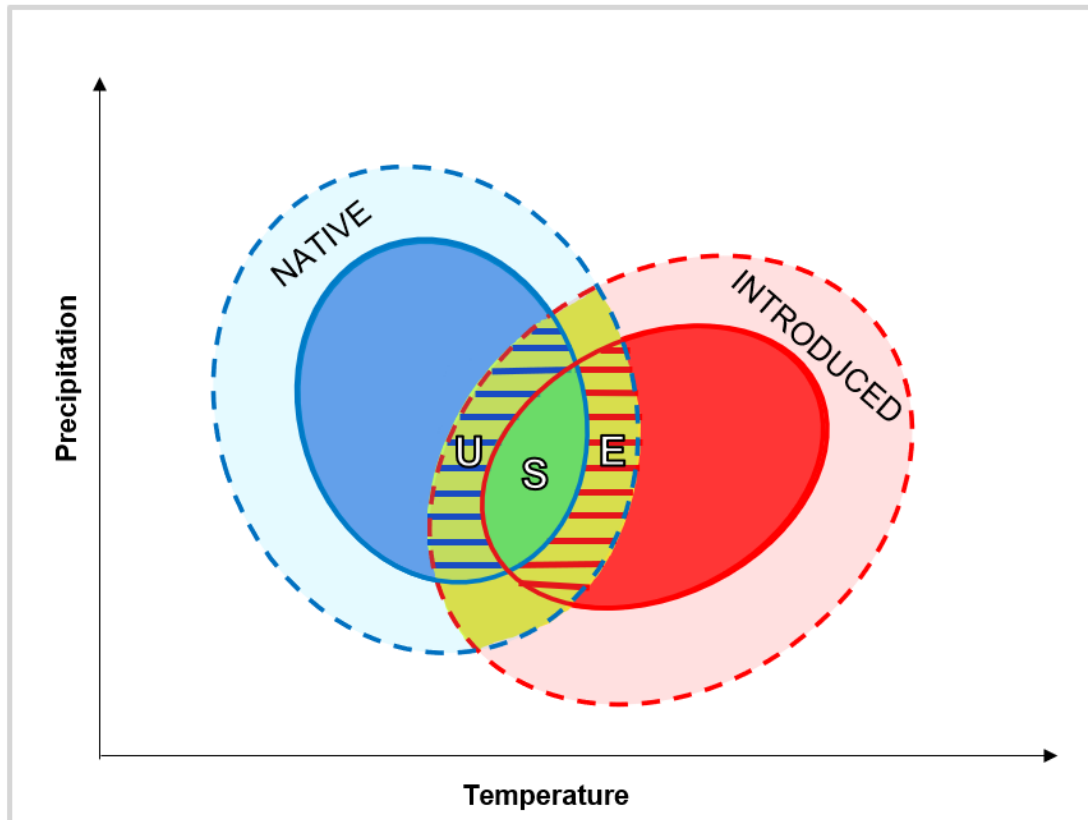
Figure 1. Conceptual figure of niche dynamics. Dashed lines indicate available climate, solid lines indicate occupied environmental conditions (realized niche). Blue represents the native range, red represents the introduced range, yellow and green represent analogous climate between ranges. (U) Niche unfilling is the proportion of analogous conditions that are occupied in the native range, but not occupied in the introduced range, (S) Niche stability is the proportion of overlapping analogous conditions that are occupied in both the native and introduced ranges, (E) Niche expansion is the proportion of the realized niche in the invaded range that is available, but not occupied in the native range. Figure adapted from Guisan et al. 2014 and Atwater et al. 2018.
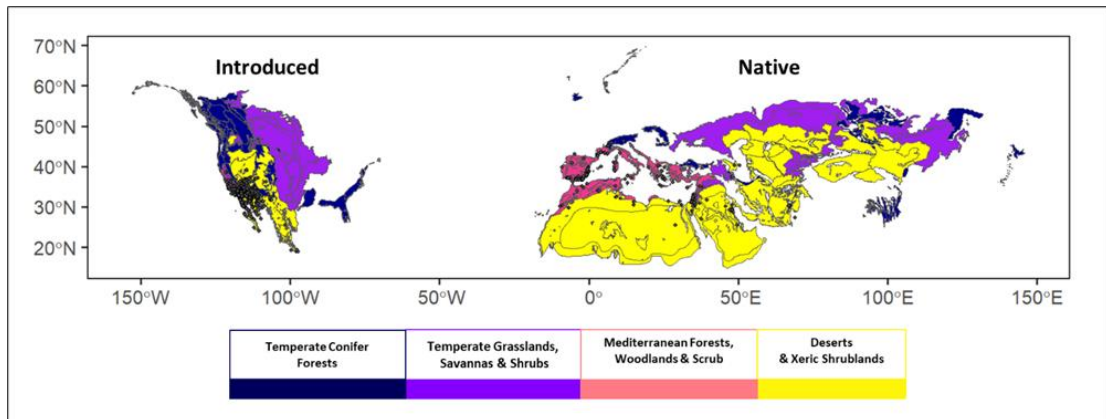
Figure 2. Study extent, showing the native and introduced occurences of *Brassica tournefortii*. Colors represent various biomes of WWF Ecoregions (Olsen et al. 2001) found within the ranges occupied by the invader
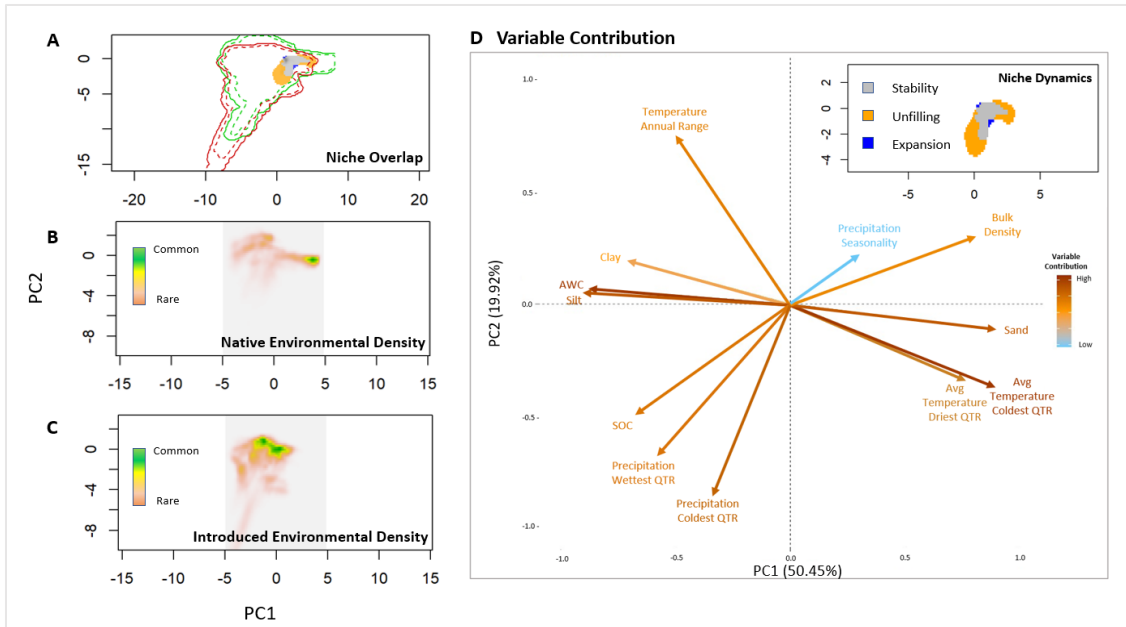
Figure 3. A) Niche overlap between analogous climate of the native (green outline) and introduced (red outline) range of *Brassica tournefortii*. Stable (gray) is occupied in both in native and introduced ranges; Expansion (blue) is occupied in the introduced but not native range (Stable + Expansion = occupied in introduced range); Unfilling (gold) is occupied in the native range, but not occupied in the introduced range. Environmental Density distribution in 2-dimensional available environmental space within the **B)** native range and **C)** introduced range. Red tones indicate an environment that is associated with lower occurrences, while yellow and green tones indicate environmental conditions that are more commonly occupied. **D)** Ordination plot for the first two principal components generated in a PCA, where warmer colors indicate higher variable contribution, while cooler tones indicate lower variable contribution. The inset provides a zoomed in image of the niche dynamics plotted in A. PC scores correspond to the ordination presented in D.
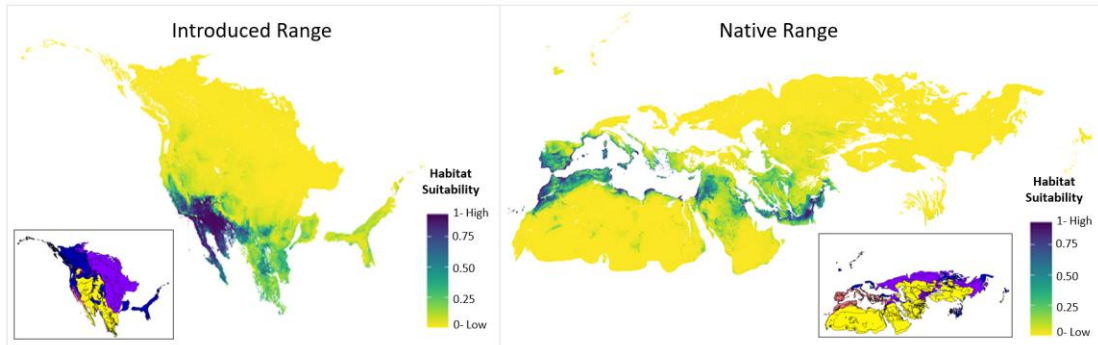
Figure 4. Habitat suitability of *Brassica tournefortii* from ensemble model predictions constructed using a weighted average based on model performance of GBM, RAF, SVM and MAXENT models. Color scale represents suitability, where yellow indicates low habitat suitability and dark blue indicates high habitat suitability. Inset maps refer to the WWF Ecoregions from Figure 2.

Table 1. Summary of environmental variables and the rationale for including them in this study

	Variable	Units	Ecological Rationale
Climatic	Precipitation seasonality (CV)	%	The coefficient of variation for monthly precipitation over the year can provide important information on whether a species is influenced by variability in precipitation.
	Precipitation of the coldest quarter	Millimeters (mm)	The total precipitation during the three consecutive coldest months of the year; precipitation and cold temperatures may influence the species distribution
	Precipitation of the wettest quarter	Millimeters (mm)	The total precipitation during the three consecutive wettest months of the year; precipitation amount during its active growing season may influence the species distribution
	Average temperature of the driest quarter	Degrees Celsius (°C)	The mean temperature of the three driest consecutive months of the year; dry season temperature seasonal hot and arid climate may influence the species distribution.
	Average temperature of the coldest quarter	Degrees Celsius (°C)	The mean temperature of the three consecutive coldest months of the year; temperature during the species active growing season may influence the species distribution.

	Temperature annual range	Degrees Celsius (°C)	The range of extreme temperature conditions (Maximum temperature of the warmest month -Minimum temperature of the coldest month) can provide information on whether a species is sensitive to seasonal temperature variation
Edaphic	Clay content	g/100g (%) Percentage of clay particles (< 0.002 mm)	Clay particles contribute to the soil's ability to hold on to nutrients for plants
	Silt content	g/100g (%) Percentage of silt particles (≥ 0.002 mm)	Silt particles provides water retention and air circulation in soil. Silty soil is considered to be one of the more fertile types of soil.
	Sand content	g/100g (%) Percentage of sand particles (> 0.05 mm)	Sand particles are large, which provide fast drainage of water and do not hold nutrients well
	Bulk density	kg/m3	Bulk density is important for infiltration and an indicator of soil health. The higher the bulk density, the more compact the soil is and higher mechanical impedance to root growth.
	Available water holding capacity (AWC)	Volumetric Fraction (Field capacity = Permanent wilting point)	AWC provides information on the maximum amount of water available in the soil for plant uptake.
	Soil organic carbon (SOC)	g/kg	SOC indicates the amount of organic matter in the soil, which contributes to a variety of soil properties that are useful for plants

Table 2. *Brassica tournefortii* occurrences by WWF Ecoregions for native and introduced ranges.

	NATIVE OCCURRENCES	INTRODUCED OCCURRENCES
ECOREGION		
Temperate coniferous forest	19	0
Temperate grasslands, savannas, and shrublands	75	103
Mediterranean forests, woodlands, and scrub	308	693
Deserts and xeric shrublands	115	6,824
TOTAL	517	7,620

Table 3. Summary of Model performance values for individual and ensemble species distribution models for *Brassica tournefortii*. Number of presences and absences for each model was 1,843. Model abbreviations: SVM= support vector machine, RAF= random forest, GBM=generalized boosted regression model, meanw = Weighted average of models based on their performance; meanthr = Averaging performed only with those cells with suitability values above the threshold at which Sorensen is highest, meansup = Average of the best models.

MODEL	AUC	TSS	JACCARD	BOYCE	IMAE
MAXENT	0.986	0.915	0.920	0.962	0.791
SVM	0.986	0.927	0.930	0.751	0.934
RAF	0.987	0.910	0.913	0.978	0.887
GBM	0.980	0.901	0.902	0.915	0.907
meanw	0.990	0.924	0.930	0.972	0.880
meanthr	0.980	0.921	0.925	0.864	0.885
meansup	0.990	0.930	0.932	0.873	0.862

Supplemental Information.

Supplementary Table 1. Details about SDM overview, data, modeling, and predictions (ODMAP) Zurell et al. 2020

ODMAP element	Contents
Overview	
Authorship	**Authors:** Clarissa Rodriguez, Santiago J.E. Velazco, M. Brooke Rose, Janet Franklin, and Loralee Larios. **Contact email:** crodr087@ucr.edu **Title:** Substantial potential for Brassica tournefortii spread in North American introduced range, despite highly conserved niche
Model objective	**SDM objective:** mapping suitable habitat for the invasive species to identify unoccupied suitable habitat **Main target output:** continuous habitat suitability index (probability of species presence)
Taxon	*Brassica tournefortii* Guan., native to Northern Africa and parts of the middle east. Invasive in North America (Southwestern U.S. and Northern Mexico)
Location	North America
Scale of analysis	- Spatial extent (Lon/Lat): - Longitude -152.9417° W - 145.825° W, - Latitude: 14.90833° N - 69.69167° N - Type of extent boundary: WWF Ecoregions - Spatial resolution: 1km - Temporal extent: period of climate normals (30 year average for 1970-2000) used for model building
Biodiversity data overview	Observation type: observations compiled from multiple agencies and individuals. 12,620 global occurrence records Response type: presence/pseudo-absence
Type of predictors	Climatic and edaphic

Conceptual model/hypotheses	Hypothesis: Climate and soils are correlated with plant distributions.
Assumptions	We assumed that all relevant predictor variables were included in our models. Since the species-environment relationship was not in equilibrium, we included native and introduced occurrence points and environmental information
SDM algorithms	**Model algorithms:** GLM, GBM, SVM, RFM, MAXENT, ensemble modeling **Model complexity:** GBM, SVM, RFM, and MAXENT were tuned using a range of hyperparameters for each model. **Ensemble modeling:** 1) using a weighted average based on Sorensen model performance (meanw), 2) using the average of the best models based on Sorensen model performance (meansup), and 3) averaging only within cells that contain suitability values above the threshold that maximizes the Sorensen index (meanth).
Model workflow	*flexsdm* package (https://github.com/sjevelazco/flexsdm)
Software	Software: R version 4.1.2 Code and data are available upon request.
Data	
Biodiversity data	**Taxon**: *Brassica tournefortii* Guan., native to Northern Africa and parts of the middle east. Invasive in North America (SW U.S. and Northern Mexico) **Taxonomic reference system**: Integrated Taxonomic Information System (ITIS) **Ecological level**: species **Data sources**: Global Biodiversity Information Facility (GBIF Secretariat, 2022; https://doi.org/10.15468/dl.ka9vk2, https://doi.org/10.15468/dl.jn8mmp). SEInet (biodiversity data accessed through Data Portal,

	http//:swbiodiversity.org/index.php, 2022-03-14), Integrated Digitized Biocollections (https://www.idigbio.org/portal, 2016) and research grade occurrence points from iNaturalist (DOI10.15468/dl.wbw2pe) from 1950-2022
	Clipping: presence and pseudo-absence data were restricted to the World Wildlife Fund's terrestrial eco-regions found within the native range of the species as indicated by occurrence data: 1) temperate conifer forests, 2) temperate grasslands, savannas, and shrublands, 3) Mediterranean forests, woodlands, and scrub, and 4) deserts and xeric shrublands.
	Potential errors and biases: Since our data was collected from several databases and was presence-only, we used a spatial block cross validation technique to remove any sampling bias and spatial autocorrelation in our dataset.
Data cleaning	Data were cleaned by georeferencing records and removing any duplicates records and records with equal coordinates. To ensure our records reflected natural habitat of the species, we added a geographic correction filter to remove records within 3 km of capital and province centroids, records within 10 km around country centroids, records within 111 km of the GBIF head quarter, records within 100 m of zoo and herbaria to exclude cultivated occurrences. Dataset contained 8,138 occurrence records.
Data Partitioning	We applied a spatial block partitioning method by partitioning our data into 12 spatially structured groups and testing 30 block grid cell sizes via block cross-validation which uses an iterative process to select the optimum grid size with the maximum environmental similarity (i.e. Euclidean distance), lowest spatial autocorrelation (i.e. Moran's I), and the minimum difference of records among groups (i.e. standard deviation- SD Velazco et al., 2019) based on our data set.
Predictor variables	• **Predictor variables:** Precipitation seasonality (CV), Precipitation of the coldest quarter, Precipitation of the wettest quarter, Average temperature of the driest quarter, Average temperature of the coldest quarter, and Temperature annual range, and six edaphic variables: Clay content (mass fraction in %), Silt content (mass fraction in %), Sand content (mass fraction in %), Bulk

	density (kg / cubic-meter), Available soil water capacity (vol. fraction), Soil organic carbon density (kg per cubic-m) ● **Data sources:** Bioclimatic variables - WorldClim database, version 1.4 (Hijmans et al. 2005); Soil variables - ISRIC World Soil Information database at a 250 m resolution (Poggio et al. 2021). ● **Data processing:** Raster data was masked and cropped to the extent of the study area (WWF Ecoregions). We used a bilinear interpolation method to create a universal resolution of 1 km for all variables. ● **Spatial resolution of raw data:** 1km, 270m ● **Projection:** NAD83
Model	
Variable pre-selection	Ecological relevance was considered when selecting variables (see Table 1)
Multicollinearity	We performed a correlation analysis to detect and eliminate pairs with a high correlation >0.75, as well as conducted variance inflation factors (VIF) tests to confirm that VIF values of each predictor variable remains below 5.
Model settings	See Supplementary Table 1 for model tuning parameters.
Threshold selection	The best hyperparameter values were based on Sorensen metrics and the threshold that maximizes Sorensen.
Assessment	
Performance statistic	In our ensembles, we excluded individual model predictions with an AUC < .95 See Table 1 for model performance summary.
Plausibility check	Janet Franklin (SDM expert and botanist) and Loralee Larios (Community ecologist) reviewed the maps to assess the validity of the spatial projections for the invasive species.
Prediction	

Prediction output	● **Prediction unit:** the probability of species habitat suitability

Supplementary Table 2. Summary of model performance and tuning parameters. Model abbreviations: SVM= support vector machine, RAF= random forest, GBM=generalized boosted regression model, meanw = Weighted average of models based on their performance; meanthr = Averaging performed only with those cells with suitability values above the threshold at which Sorensen is highest, meansup = Average of the best models. Number of presences and absences for each model was 1,843.

Model	MAX	SVM	RAF	GBM	meanw	meanthr	meansup
Threshold	max_ soren sen	max_ soren sen	max_ soren sen	max_ soren sen	max_ sorensen	max_ sorensen	max_ sorensen
Threshold Value	0.393	0.513	0.614	0.461	0.396	0.224	0.276
TPR mean	0.969	0.968	0.966	0.964	0.974	0.967	0.974
TPR SD	0.014	0.02	0.006	0.012	0.015	0.015	0.015
TNR Mean	0.946	0.958	0.941	0.931	0.95	0.954	0.955
TNR SD	0.012	0.018	0.02	0.015	0.015	0.015	0.016
SORENSEN Mean	0.958	0.963	0.954	0.948	0.963	0.961	0.965
SORENSEN SD	0.006	0.011	0.011	0.013	0.011	0.014	0.01
JACCARD Mean	0.92	0.93	0.913	0.902	0.928	0.925	0.932
JACCARD SD	0.012	0.02	0.02	0.023	0.02	0.025	0.019
FPB Mean	1.84	1.859	1.826	1.804	1.856	1.849	1.865
FPB SD	0.023	0.04	0.039	0.045	0.04	0.05	0.037
OR Mean	0.031	0.032	0.034	0.036	0.026	0.033	0.026
OR SD	0.014	0.02	0.006	0.012	0.015	0.015	0.015
TSS Mean	0.915	0.927	0.907	0.895	0.924	0.921	0.929
TSS SD	0.013	0.021	0.022	0.026	0.021	0.028	0.02
AUC Mean	0.986	0.986	0.987	0.98	0.989	0.982	0.988

AUC SD	0.002	0.008	0.004	0.006	0.004	0.011	0.003
BOYCE Mean	0.962	0.751	0.978	0.915	0.972	0.864	0.873
BOYCE SD	0.03	0.162	0.013	0.049	0.02	0.083	0.09
IMAE Mean	0.791	0.934	0.887	0.907	0.88	0.885	0.862
IMAE SD	0.019	0.013	0.011	0.016	0.013	0.018	0.016
Regularization multiplier	0.100	-	-	-	-	-	-
Feature class	qhp	-	-	-	-	-	-
C	-	6	-	-	-	-	-
Sigma	-	0.175	-	-	-	-	-
mtry	-	-	1	-	-	-	-
# trees	-	-	500	80	-	-	-
Shrinkage	-	-	-	0.700	-	-	-
n.minobsinnode	-	-	-	15	-	-	-

* Column Descriptions: TPR =True-Positive Rate; TNR = True-Negative Rate; FPB=The threshold at which the F-measure on presence-background data is the highest; max_sorens= The threshold at which Sorensen is highest; OR= Omission Rate; TSS= True Skill Statistic; AUC= Area under Curve; BOYCE= Continuous Boyce Index; IMAE=Inverse Mean Absolute Error. *SD= standard deviation.
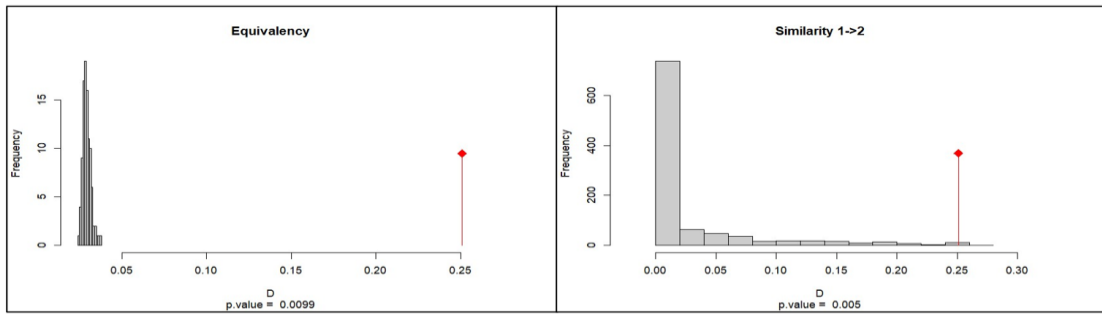
Supplementary Figure 1. Histograms depicting the observed overlap between the native and invaded niche to the overlap between two randomly simulated niches after 1,000 simulations to test for niche equivalence (left) and niche similarity tests (right). Red line indicates the overlap between the native and introduced range (25%).
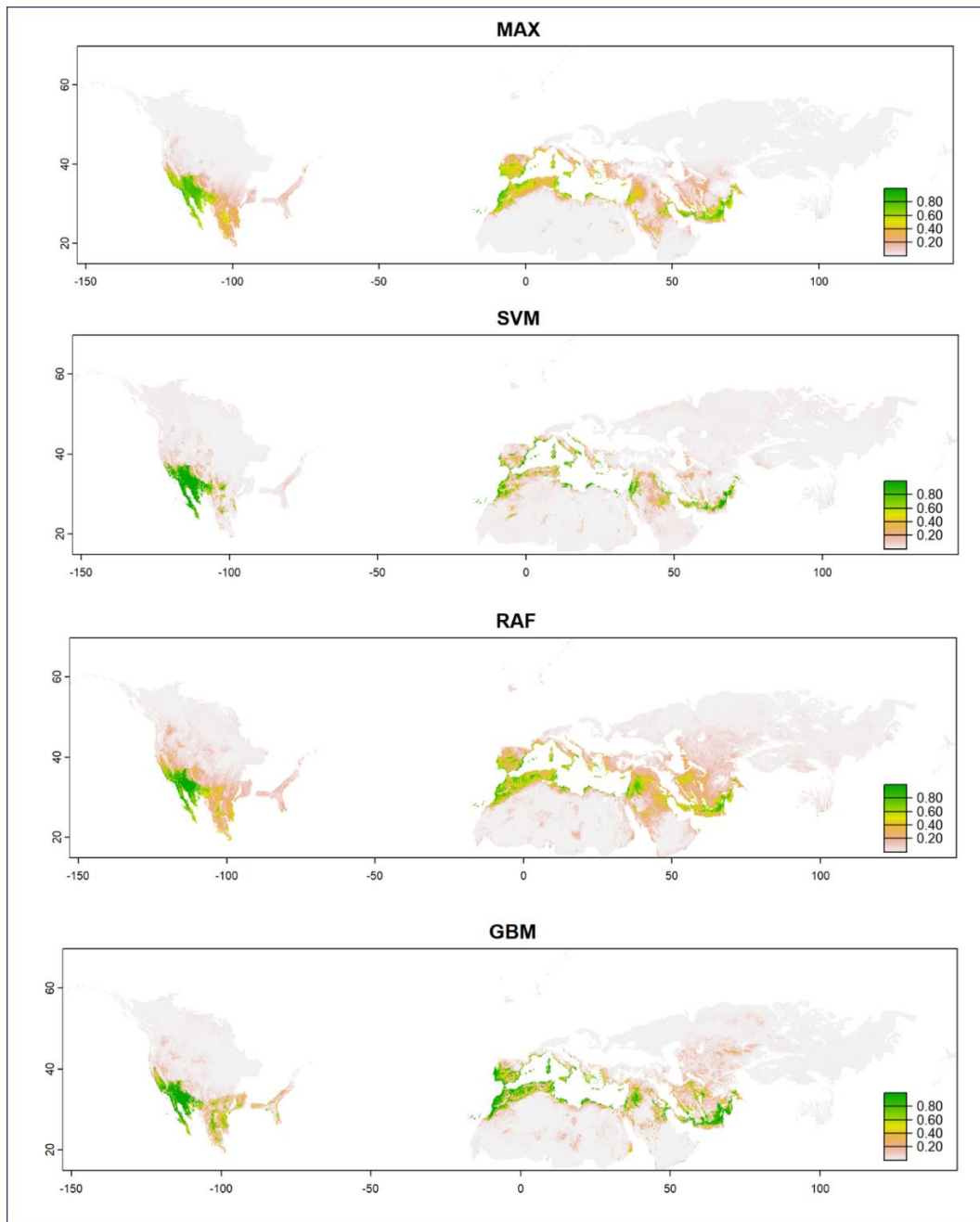
Supplementary Figure 2. Species distribution maps (SDM's) for each individual algorithm: Maximum Entropy (MAX), Support Vector Machine (SVM), Random Forest (RAF), and General Boosted Regression (GBM) models. Color indicates the suitability of habitat, where green indicates high suitability, orange indicates low habitat suitability, and gray indicates no suitability.
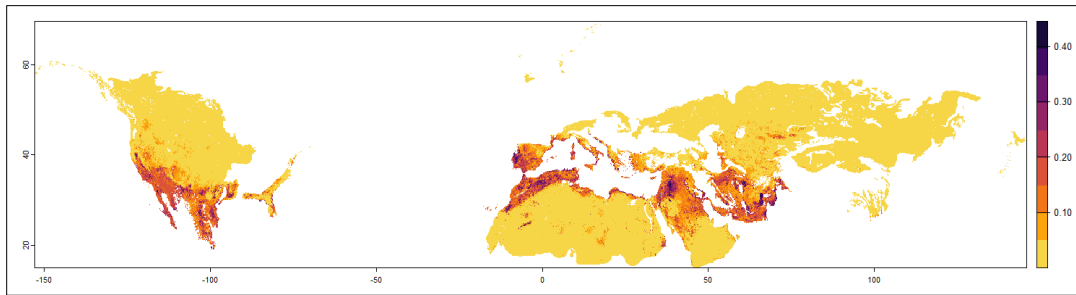
Supplementary Figure 3. Uncertainty map showing the standard deviation across SDM's shown in figure S2.

CHAPTER 2

Magnitude and frequency of invasion booms as drivers of shifts in community synchrony and stability in an aeolian sand habitat

Abstract. Invasive species are one of the leading drivers of global change, altering community structure and ecosystem function, posing a significant threat to global biodiversity. To better predict community responses to future invasions, it is crucial to evaluate how invasive species may be impacting recipient communities, especially in historically uninvaded systems such as drylands. While invader abundance is typically used as the main predictor of community impacts, it may not effectively capture invader impacts in systems that experience cyclical dynamics (i.e., boom-bust patterns), as invader abundance and resident community composition will vary from one year to the next. Further, in dryland systems, variable precipitation can lead to a low number of species within a year and variable total species over time, rendering univariate metrics like richness and diversity, inadequate for evaluating how communities may be responding to invaders over time. To capture temporal shifts in invaded communities, using longer-term responses such as community synchrony and stability may be more suitable metrics to evaluate community impacts. This study leverages a long-term dataset to assess the temporal dynamics of a dominant annual invader, *Brassica tournefortii*, and evaluate how attributes of this invaders boom-bust dynamic (i.e., invasion level, boom frequency and magnitude) may influence the synchrony and stability of invaded stabilized sand dunes communities. We found that although invasion level, which was based on abundance alone, mediated the dynamics of invasion regimes, attributes that captured the temporal effects of the invader proved to be stronger predictors of changes in communities. Specifically, as the frequency and magnitude of invader booms increased over time,

the community became destabilized due to a decrease in species asynchrony. This study highlights how utilizing long-term metrics that reflect abundance changes over time can improve evaluations of invader impacts on invaded communities in dynamic systems.

Introduction. Biological invasions are a leading driver of global change, threatening biodiversity by altering disturbance regimes (Mack & D'Antonio, 1998; Miller et al. 2021), community structure (Ortega & Pearson, 2005; Castro-Diez et al. 2016), and ecosystem function (D'Anotnio & Vitousek, 1992; Vila et al. 2011). Assessing the impacts of invasive species on recipient communities is critical for being able to predict how communities may respond to future invasions. Invader abundance tends to scale positively with impact (Parker et al. 1999; Pearse et al. 2019); therefore, quantifying invader impacts is most commonly done via abundance-impact relationships, where abundance of the invader is the sole predictor of native or whole community health metrics such as species richness, evenness, and diversity. However, for low-productivity systems where species diversity and richness tend to be low, it may be more difficult to detect or interpret a significant invader impact. Additionally, in highly variable systems, where environmental fluctuations can elicit differential responses from species due to differences in life history traits, tracking invader impacts may be more challenging, especially where communities are composed of a few dominant species, and many rare or transient annual species (Levine and Ress, 2004; Schwinning & Sala, 2004). These conditions may result in invaders that experience cyclic population dynamics (i.e., boom-bust patterns, Strayer et al. 2017) that will require alternate approaches to evaluating invader impact. Moreover, given the low richness and variable community dynamics that are inherent in some dryland systems, an alternate metric is needed for these systems that can better capture invader impact. Therefore, quantifying longer term community response metrics such as community synchrony and stability may better capture the temporal components that are inherent in invasion dynamics (Crystal-Ornelas & Lockwood, 2020; Valencia et al. 2020).

Classically, in abundance-impact studies, invader abundance is often used to assign levels of invasion (i.e., low, moderate, high); however, in systems where an invader exhibits cyclic population dynamics (i.e., boom-bust patterns, Strayer et al. 2017) using temporally implicit metrics can help elucidate underlying dynamics that may be driving patterns of invader populations over time (Tekiela & Barney, 2017). Abundance-based attributes that deconstruct temporal abundance dynamics have been successfully used to determine when an invader with cyclical dynamics is likely to collapse or rebound (Aagaard & Lockwood 2016). For instance, Aagaard & Lockwood, 2016 assessed non-native bird population dynamics using the severity (i.e., magnitude of single abundance decline) versus average abundance of bird populations and the duration (i.e., length of time elapsed) of a population decline to determine if the population experienced a population collapse and if it was likely to recover from declines that exceeded a certain abundance threshold (i.e., busts). An invader population collapse might indicate that the impact of an invader has lessened, but in systems where an invader exhibits cyclical dynamics, its population may recover and continue to exert impacts on the recipient community. This approach of breaking down the temporal attributes of an invader's dynamics can be similarly used to understand the impact of an invader and uncover additional drivers of community-level impacts on invaded communities, in systems that experience cyclical vegetative composition dynamics and have generally low productivity.

Within the context of cyclical systems, invader abundance dynamics can be broken down into several attributes: the magnitude of a boom event, the frequency of invader boom events within a community, as well as the mean return interval of a boom events over time (Fig. 1). Together these attributes can be used to describe an invasion regime. To properly gauge the impact of a boom-bust invader, the magnitude of the boom must be considered. It is widely recognized that high levels of invader abundance can have detrimental effects on the native

community. Hence, analyzing the degree of invader abundance booms provides insights into the potential negative alterations that may affect the native community (Strayer et al. 2017). Importantly, an invader's boom should be scaled to baseline native vegetation abundances to better understand the relative impact of various invader boom magnitudes on community dynamics, especially in environments where there is high interannual variability in the vegetative composition. Long-term impacts of an invader may be better captured by the frequency and mean return interval of boom events, as they are predictive of carryover effects (i.e., event(s) during a previous season that affect individuals during the current season) that accumulate over time to impact community trajectories (Ryo et al. 2019). For instance, frequent invader booms may contribute to both increased invader propagules and decreased native propagule supply over time (Gioria & Pysek, 2015), shifting the community into an invader dominated community state. Analyzing the average duration between boom occurrences (i.e., mean return interval) can also provide valuable insights into how community trajectories may differ based on the time allowed to recover from each event. This may be particularly valuable for invasive species that establish legacy effects, such as pathogen loading (Mangla & Callaway, 2007; Flory & Clay, 2013), elevated soil nitrogen (Yelenik & D'Antonio, 2013; Hobbie, 2015), and allelopathy (Qu et al. 2021; Kalisz et al. 2021), as a shorter duration may facilitate the accumulation of invader impacts over time. Moreover, the magnitude of invader booms and frequency may work in tandem to create interactive or additive responses that overwhelm native ecosystem resistance and result in the persistence and abundance of the invader (Ryo et al 2019; Panetta et al. 2019). Therefore, to fully comprehend the impacts of invaders on recipient communities, it is crucial to use effect and response metrics that respectively capture the impacts of invaders and changes in community dynamics over time.

Despite the potential for invasive species impacts to vary and potentially accumulate over time, invader impact studies are typically conducted over short time scales and use response metrics that may not fully capture the full range of invader impacts. A recent meta-analysis of invader impact studies found that out of 2,293 case studies, 74% of studies were conducted over short temporal scales, ranging from 0-3 years, with less than 150 studies covering invader impacts past 10 years (Crystal-Ornelas & Lockwood, 2020). Additionally, Crystal-Ornelas & Lockwood (2020) found that community response metrics were heavily skewed toward including metrics that only required one measurement during one time point (i.e., species diversity and abundance). However, in dryland systems where species richness tends to be low at a given site, short-term metrics such as diversity may not be sensitive to overall changes in species number or identity (Bradley et al. 2019; Valencia et al. 2020). In systems with high environmental variability, asynchrony in species abundances over time is key to maintaining biodiversity (Chesson, 2000; Angert et al. 2009); therefore, metrics that occur over longer temporal scales are needed to fully capture the impact of an invader on the recipient community. Invasive species can destabilize communities by reducing biodiversity and altering species-level interactions such as synchrony (Valone & Balban-Feld, 2018; Vetter et al. 2020). It is critical for metrics to not only capture changes in biodiversity within communities but to also capture changes in the mechanisms that confer stability to ecosystem functioning (Loreau and de Mazancourt, 2013; Hallett et al. 2014) and contribute to community resistance and resilience to environmental stressors such as species asynchrony.

Here, we use a longitudinal study to ask, how do invasion regime attributes of an invasive annual plant, *Brassica tournefortii* influence community synchrony and stability in a stabilized sand field system? We predict that attributes that capture temporal and carryover effects of our focal invader will be better predictors of changes in community synchrony and stability compared to traditional metrics of invader abundance level attributes.

Methods.

Study Site – This observational study utilized plant community data collected in stabilized sand fields located within the federal Coachella Valley National Wildlife Refuge (33.7979973°, -116.3251516°) from 2003 to 2019. These stable sand fields are characterized by high temporal variability, and consist of a variety of interspersed native forbs, grasses and shrubs.

Focal Invader – Brassica tournefortii, sahara mustard, is an annual winter forb native to the Mediterranean Basin and parts of the Middle East. This species is thought to have been introduced into North America via the palm tree trade in Coachella, CA, USA during the early 20th century (Minnich and Sanders 2000). *Brassica tournefortii* is a common invader throughout North American drylands and is the dominant invader within Coachella Valley's stable sand fields (Barrows et al. 2009). This species exhibits "boom-bust" dynamics in this system where some years the invader is very prevalent, and other years the abundance is very low (VanTassel et al. 2014).

Study Design & Sampling – We leveraged long-term observational belt transects that were established in 2002 as part of the Coachella Valley Multiple Species Habitat Conservation Plan Monitoring Program (Allen et al. 2005). Within stable sand field habitats, 19 belt transects were arranged as 100 m x 10 m (0.1ha) rectangles. Within each belt transect, four 1 m^2 quadrats plots are spatially grouped within a cluster (3 clusters per transect: A,B,C; n=12 plots/transect, Fig. 2). To capture community composition, plots were alternated along the center line of the transect for a total of 228 plots across the 19 transects (Fig. 2). Due to some plots missing vegetation data for several years, we reduced our dataset to 226 plots in our study. Vegetation within these plots were surveyed annually from 2003-2019 using stem counts and visual estimates of cover for each

64

species present within the aboveground vegetation during peak biomass in the spring, (March-April), dependent on phenology. Here, we focus on the visual estimates of plant cover to quantify invasion regime attributes.

Quantifying attributes of invasion regime

We used our long-term visual estimates of vegetative cover data from 2003-2019 to quantify the following attributes of *Brassica tournefortii's* invasion regime: 1) invasion level, 2) frequency of abundance booms, 3) mean return interval between booms, and 4) dominant magnitude of booms. To account for the spatial structure of our observational belt transects, we assigned the invasion level (i.e., low, moderate, high) to each cluster (i.e., A, B, C) for every transect. First, we took the non-zero temporal average (2003-2019) of sahara mustard percent cover within each of the $1m^2$ plots. For each of the four plots within a cluster, we assigned one of the following categories: 'Low'= 1-14.99 % cover per plot, 'Moderate' = 15-29.9 % cover per plot, and 'High'=30-40 % cover per plot. We then identified the mode (i.e., the categorical range of sahara mustard abundance that appeared most frequently) to determine the level of invasion for each cluster, resulting in 56 low invasion plots, 116 moderately invaded plots, and 54 highly invaded plots. To verify that spatial autocorrelation was not present within our assigned invasion level categories, we calculated Moran's I Autocorrelation Index using the 'ape' package in r (Paradis, 2019).

To assess a baseline for dominant native species vegetative cover within this low-productive system, we subsetted our long-term data to only include plots where sahara mustard was absent from the community. We then identified the mode of the raw maximum % vegetative cover of the dominant native annual native species (*Abronia villosa, Chylismia claviformis,* and *Oenothera deltoides*) in this system, which was 60% cover. We used this value to define the parameters for what constitutes a 'boom' in this system. We defined a 'Type B boom' as having an amplitude of at least 60% raw cover of *Brassica tournefortii*. We defined a 'Type A boom', which is of lower

magnitude, for plots that experienced at least half of a 'Type B boom' (30% $\geq$ x $\leq$ 59% *Brassica tournefortii* cover). Lastly, we classified plots as 'no boom' if *Brassica tournefortii* cover remained below 30% vegetative cover (0% $\geq$ x $\leq$ 29% cover). Notably, sahara mustard may be present in "no boom" plots but it is not exhibiting a large population increase.

To calculate the frequency of booms, we summed up the total number of both 'Type A boom' and 'Type B boom' occurrences per plot throughout the study extent, resulting in 5 levels (0-4). To quantify the mean return interval of booms, we calculated the number of years between the max abundance between each boom occurrence and divided the sum of years by the frequency of booms. Since we had plots that experienced no booms, we assigned a value of 16 years, which was the extent of our study period, to those plots with a boom frequency of 0. Similarly, for plots that only experienced a boom frequency of 1, we assigned a value of 10 years, which was the average time lapsed after a single boom occurrence. To identify the dominant magnitude of boom for each of our 226 plots, we assessed the number of times a 'Type A boom' or 'Type B boom' occurred within each plant community throughout the study extent. In the case where plots experienced an equal number of 'Type A boom' and 'Type B boom', we categorized those plots as having an 'even' dominant magnitude of boom (e.g., 1 'Type A boom' and 1 'Type B boom'). As a result, four categories of invader boom magnitudes were identified, increasing in invader abundance with each sequential level (i.e., no boom, Type A boom, even, and Type B boom).

Quantifying Community Responses

To assess community-level responses, we calculated species richness as the sum of all species present within the 1m^2 plot for each year surveyed. Additionally, to account for species richness and evenness within a plot, we calculated the Shannon-Weiner index (*H*) using the 'vegan' package (Oksanen et al. 2022) for each year.

To calculate synchrony, we used the 'Loreau' option in the community_synchrony() function

from the 'codyn' package in R (Hallett et al. 2016), which compares the variance (σ) of

aggregated species abundances within a single community (X_T) to the summed variances of

individual species abundance (X_i) found within that same community. We calculated community

synchrony for each plot using the following equation: $Synchrony = \frac{\sigma(X_T)^2}{(\Sigma_i \sigma_{X_i})^2}$, where $x_T(t) =$

$\sum_{i=1}^{N} x_i(t)$ denotes plant abundance for the ith species within a community over time. This

measurement enables the comparison of communities with varying species richness and offers a

standardized way to assess synchrony. A score of 0 indicates complete asynchrony, while a score

of 1 indicates perfect synchrony (Loreau & Mazancourt 2008). To calculate community stability,

we applied the community_stability() function from the same package which consolidates species

abundances in each plot and time frame to calculate stability as the temporal mean of the study

extent (2003-2019) divided by the temporal standard deviation (μ/σ, Lehman and Tilman 2000).

Analyses

To assess whether invader dynamics experienced by a community varied by invasion level, we

first performed Pearson's Chi-Squared X^2 tests on histograms of invasion attributes using the

chisq.test() function in base R. For the first X^2 test, we compared the frequency of booms (0-4)

present within each level of invasion (low, moderate, high). For the second X^2 test, we compared

the mean return interval of boom occurrences throughout the study extent (2003-2019), between

each invasion level (low, moderate, high). For the third X^2 test, we compared the dominant boom

magnitude (no boom, Type A boom, even, Type B boom) present within each level of invasion

(low, moderate, high).

Next, to assess traditional metrics of community-level responses (i.e., species richness and

diversity) to invasion, we created linear-mixed effect models using the 'lme4' package in R

(Bates et al. 2015). For the first model, we fit Shannon-Weiner index as the response variable, with invasion level (low, moderate, high) as a fixed factor, with cluster nested within transect as a random factor. For the second model, we used the same model structure as above, but replaced the Shannon-Weiner index with species richness as the response variable. We then compared individual treatment levels in our models using Tukey's HSD post-hoc tests.

To assess how attributes of *Brassica tournefortii's* invasion regime influence community synchrony and stability across an invasion gradient, we took a backwards stepwise model selection approach with linear-mixed effect models. We created two separate global models, one with community synchrony as the response variable and the second with community stability as the response variable. Within these global models, the following were included as fixed factors: frequency of booms (0-4), dominant magnitude of boom (no boom, Type A boom, even, Type B boom), mean return interval between booms, invasion level (low, moderate, high), with all possible interactions, with cluster nested within transect as random factors. To check for multicollinearity among our predictor variables, which were derived from plant abundance values, we used the 'car' package in R to calculate a variance-inflation factor (VIF) value for each predictor variable in our models. If variables had a VIF value $\leq$ 5, low correlation among variables was confirmed and were kept within our models. During model selection, models where mean return interval between booms was removed resulted in the lowest AIC values. As a result, in our first model, we used community synchrony as the response variable, with frequency of booms (0-4), dominant magnitude of boom (no boom, Type A boom, even, Type B boom), and invasion level (low, moderate, high) and their interactions as fixed factors. We included cluster nested within transect as random factors. We used the same model structure for our second model, replacing community stability as the new response variable. We used Tukey's HSD post-hoc tests to compare individual levels of treatment in our models. Lastly, to test if attributes of an invasion

regime (i.e., dominant boom magnitude) are predictive of community stability, we created a third

model where we used community stability as a response variable, with community synchrony,

dominant boom magnitude, and their interactions as fixed factors and cluster nested within

transect as a random factor. To meet assumptions of normality, we log-transformed and added a

constant to our community stability and community synchrony data.

Results.

Attributes of Brassica tournefortii's *invasion regime*

We observed that attributes of an invasion regime are mediated by underlying level of invasion

(Fig. 3). Firstly, the frequency of booms ($X^2_{(8, 226)} = 96.583$, p-value < 0.001; Table 1) strongly

varied by invasion level, with low-level invasion plots experiencing fewer boom frequencies

compared to moderate and high levels of invasion. For the low level of invasion, the frequency of

booms never exceeded a frequency of 2 booms throughout the study extent, while moderate and

high levels of invasion did experience frequencies of 3 and/or 4 (Fig.3A). The mean return

interval of booms also differed among invasion levels ($X^2_{(18, 226)} = 7\ 4.755$, p-value < 0.001; Table

1), where low level invasion plots on average were characterized by longer intervals than

moderate or high invasion level plots. Plots with low levels of invasion had a high prevalence of

mean return intervals of 16 years, representing the high number of 'no booms' present within this

level of invasion (Fig. 3A-B). Further, moderately invaded plots experienced the highest

prevalence of mean return interval of 10 years, representing the high frequency of plots that only

experienced 1 boom throughout the study extent. In contrast to low level invasion plots, we found

that moderate and high-level invasion plots experienced frequent mean return intervals ranging

from 1-6 years apart, suggesting these plots had less time to recover from invader boom

occurrences (Table 1, Fig. 3). Furthermore, we found that the dominant magnitude of booms ($X^2_{(6, 226)} = 74.755$, p-value < 0.001; Table 1) also varied greatly by level of invasion, with moderate

invasion levels containing a higher prevalence of varying magnitude of boom events compared to low and high invasion level plots. Within low levels of invasion, we observed that communities experienced the least amount of invader 'Type A' and 'Type B' booms, while experiencing the highest prevalence of 'no booms' throughout the study extent (Fig. 3C). Both moderate and high invasion level plots were both dominated by 'Type A' booms magnitudes; however, moderate invasion level plots experienced the highest frequency of the highest magnitude, 'Type B' booms.

Diversity & Richness

Within stable sand fields, we observed that the mean Shannon diversity/m^2 decreased as the level of invasion increased (p-value < 0.001, Table 2, Fig. 4A), albeit with small differences in average Shannon diversity (< 0.5 species/m^2) between low level and high level invasion plots. Species richness on the other hand did not significantly differ between invasion levels (p-value = 0.091, Table 2, Fig. 4B), as all invasion levels contained on average species richness between 3.5-3.8.

Community Synchrony

We found that community synchrony was influenced by the main factors of boom frequency (p-value = 0.003) and the dominant magnitude of boom (p-value = 0.043), but not by the level of invasion (p-value = 0.695), nor any interactions between factors (Table 3, Fig. 5). We found that a frequency of 1 boom was enough to significantly increase the synchrony of the community compared to plots that had no booms, which exhibited low synchrony and thus higher asynchrony (post-hoc, p = 0.002). We also found that plots that received the highest frequency of booms (e.g., 4), had significantly higher values of community synchrony compared to no booms (post-hoc, p = 0.013) and 3 booms (post-hoc, p = 0.028). However, plots that experienced either 2 (post-hoc, p = 0.935) or 3 booms (post-hoc, p = 0.811) did not differ from plots that received 0 booms throughout the study extent, likely due to having lower variation of responses (SD < 0.09)

compared to frequencies of 1 and 4 which had higher variation in responses (SD>12). When evaluating responses of community synchrony to cyclical dynamics, we observed that plots that never experienced abundance booms throughout the study extent (i.e., frequency of 0, or magnitude of 'no boom') contained the lowest values of community synchrony (i.e., higher asynchrony). However, for plots that experienced cyclical boom dynamics, we observed a trend of increasing community synchrony with increasing magnitude of the dominant boom.

Community Stability

We found that community stability was influenced by the main effects of the frequency of booms (p-value = 0.004) and the dominant magnitude of boom (p-value < 0.001), but not by the level of invasion (p-value = 0.646), nor any interactions between factors (Table 3, Fig. 6). Similar to the community synchrony response, we found that a boom frequency of 1 (post-hoc, p = <0.001) was enough to shift temporal dynamics by significantly lowering community stability compared to plots that did not experience abundance booms throughout the study extent. However, plots that experienced boom frequencies of 2 (post-hoc, p = 0.711) or 3 (post-hoc, p = 0.229) did not significantly differ from plots that had a frequency of 0 booms. Plots that experienced 4 distinct abundance booms (highest frequency of booms) throughout the study extent resulted in significantly lower community stability compared to undisturbed plots (post-hoc, p=0.039). When we assessed how the dominant magnitude of invader boom influenced stability, we found that plots that never experienced abundance booms contained the highest levels of community stability, followed by a sequential decrease in community stability as the dominant booms increased in magnitude.

We found strong evidence that community synchrony ($p < 0.001$), dominant magnitude of booms ($p < 0.001$) and their interactions ($p < 0.001$) are strong predictors of community stability (Table 4). As the dominant magnitude of boom increased, the relationship between community synchrony and stability, eroded and became less steep, with 'no boom' plots containing the largest slope and y-intercepts, and 'Type B boom' plots containing the smallest slope and y-intercept (Fig 7).

Discussion. Evaluating the impact of invaders with cyclical population dynamics in low resource systems requires careful consideration of which metrics to use, as short-term metrics (i.e., richness, diversity) may not capture changes in species identity or abundances over time compared to longer-term metrics (i.e., synchrony). Here, we assessed a variety of invasion regime attributes as drivers of changes in community dynamics over time (i.e., synchrony and stability). Although we found that invasion regime dynamics varied by underlying invasion level, we found that temporal attributes of boom frequency and dominant boom magnitude are much stronger predictors of changes in communities than invasion level. Our research revealed that as invaders experienced more frequent and stronger booms, community synchrony also increased. This in turn led to a decline in community stability over time in communities that experienced stronger or more frequent booms. Using a longitudinal approach, we demonstrate that univariate response metrics are not suitable estimates of invader impacts for temporally variable systems. Our findings suggest that focusing on measures that account for fluctuations in species abundances over longer temporal scales may be more suitable for quantifying species and community responses to invader impacts in more dynamic systems.

Capturing biologically significant changes in low-resource systems may require moving beyond univariate metrics to more accurately interpret invader impacts on dynamic communities. In our study, we found that species diversity declined as the level of invasion increased, which is

consistent with the literature of classic invader abundance-impact studies (Bradley et al. 2019).

However, using this metric as a response variable only detected small differences between the

low and high levels of invasion, and no differences between medium levels of invasion. These

findings suggest that diversity in this low-resource system may be too low at a given time point to

capture changes. Similarly, species richness did not vary between invasion levels, potentially

leading to the erroneous conclusion that the small differences across the invasion gradient are not

biologically meaningful, and the incorrect perception of the invader as low-risk. Moreover,

invasive species can alter community aspects that impact the ecosystem without necessarily

reducing species diversity or richness. For instance, Fenesi et al 2023 found high variability in the

impact on resident communities among invasive herbaceous plants. As a result of the variability

of invader impacts, changes in diversity were found to be overall negligible when the impact of

all species were assessed (Fenesi et al. 2023). Further, much of this context dependency has been

found to be directly linked to invader characteristics (Hejda et al. 2009), highlighting the

importance of evaluating multiple attributes of the focal invaders attributes to capture the full

range of potential impacts the invader can have on a system. Our long-term analysis of species

synchrony and stability indicates that this invader is strongly impacting community dynamics,

despite overall no to small differences and richness, and suggests that classic response metrics for

invader impact studies (e.g., species diversity and richness) may be insufficient to capture the full

range of dynamics exerted by the invader on the recipient community.

In temporally variable environments, such as deserts, high asynchrony (i.e., low

synchrony) in species responses helps maintain species diversity by limiting competition between

species through time (Chesson, 2000; Letten et al. 2018). In our study, plots that experienced

cyclical invasion patterns exhibited increased synchrony and decreased stability, with the

synchrony of the community increasing in tandem with both the frequency and intensity of

invader booms. This suggests that the resident species in the invaded communities are responding to attributes of the invasion regime and that the invaders are likely hindering the ability of species to avoid competition through asynchronous dynamics (Wagg et al. 2022). The disruption of species asynchrony is further supported by the shifting negative relationship between synchrony and stability that we observed as the intensity of booms increased, indicating that as community synchrony increases (i.e., asynchrony decreases), the possibility for functionally important or dominant species may be lost, resulting in declines in stability and ecosystem functioning over time (Valencia et al. 2020; Vetter et al. 2020). Overall, we found that integrating temporal changes in community composition through measures of synchrony and stability revealed strong community shifts in responses to invasion attributes; thus, incorporating metrics that account for changes over time in dynamic ecosystems are key to detecting invader impacts. Overall, accounting for carryover effects in invasive species management may be crucial in understanding the long-term implications of invader booms and developing effective strategies to prevent their recurrence.

The resilience of invaded communities to invader impacts may be influenced by stress-tolerant life history strategies and functional diversity. Many studies have quantified the impacts of invasive species; however, a large portion of those studies have been carried out on short time scales (Crystal-Ornelas & Lockwood, 2020). Our long-term approach allowed us to identify areas of community resistance and potential thresholds to invader impacts on community synchrony and stability. We also found a degree of resilience within invaded communities, as the temporal stability incrementally recovered from the first initial boom dynamic, until reaching a threshold (i.e., four booms) that triggered a shift within the community. The resilience and resistance observed within these communities may be in part due to the stress-tolerant life history strategies that many native species within this system possess (Battisti, 2021; Chambers et al. 2023). For

instance, species that evolved in stressful environments, such as deserts, may often be tolerant to abiotic stressors (e.g., extreme temperatures, low resource availability), potentially increasing the ability of species to individually resist change through their long-lived seedbanks that may act as a buffer to environmental changes (Adler et al. 2014; LaForgia et al. 2018; Maestre et al. 2021). Although we did not include it here, evaluating diversity in functional traits within communities may help further explain why some communities may be more resistant to invader impacts than others (Fenesi et al. 2023). In systems, such as drylands, where abiotic factors (i.e., temperature and precipitation) are strong filters of community assembly, redundancy in species functional traits may serve as a property of ecological resistance, buffering loss of ecosystem functioning (Spasojevic et al. 2018; Maestre et al. 2021). However, it is important to note that stress-tolerant strategies may actually make certain species more vulnerable to the negative effects of invasive species, due to life history tradeoffs. For instance, species that grow slowly but have high stress tolerance may be outcompeted by invasive species that have more aggressive life history strategies, such as being strong competitors for resources or colonizers in highly disturbed environments (Catford et al. 2018). Depending on the functional diversity of the community, this tradeoff in life history strategies may result in the loss of functionally important species within the community, resulting in the eventual loss of ecosystem functioning over time (Valone et al. 2019). While we observed potential threshold dynamics associated with the frequency of invader booms, other attributes may exhibit linear relationships with stability, suggesting the potential for accumulation of impacts over time.

Overall, our study emphasizes that evaluating the full range of invader impacts on communities may require a variety of metrics that capture temporal effects, especially in more dynamic systems where species responses may not be straightforward. In this paper, we touch on several attributes (i.e., invader boom frequency, mean return level, boom magnitude) that

contribute toward shifts in community dynamics that contribute to community stability. However, our list of invasion regime attributes is not exhaustive, metrics, such as the duration of invader booms (e.g., how many consecutive seasons did the boom last for) may allow time for legacies to develop to impact native communities. As Strayer et al. (2017) suggests, including multiple attributes of boom-bust dynamics may further advance our understanding of underlying mechanisms (e.g., resource depletion, competition, disturbance-mediated) driving invader impacts over time, allowing us to more strategically design and implement invader control strategies. For instance, identifying a major driver of invader impacts (e.g., dominant magnitude of invader boom) can inform where to prioritize invasive plant management resources, which are often limited, where carryover effects are likely to accumulate to prevent further booms. Lastly, evaluating multiple attributes of invasion regimes can also help identify areas that may be feasible for eradication or control, where invasion level may be low (i.e., low average invader abundance), but community impacts may be high, providing the opportunity for asynchronous native species to recolonize over time.

As ecosystems continue to grapple with ongoing climate change and other drivers of global change (e.g., biological invasions), predicting how species and communities may respond to future stressor continues to be a challenge. This challenge may be exacerbated if drivers of global change such as invaders erode a community's internal mechanisms for stability. Here we show that it is important to think of other invader effect and community response metrics beyond classic invader abundance-impact studies to estimate impacts of invaders with cyclical dynamics. Failure to track invader impacts can have negative implications for land management and restoration efforts (Weidlich et al. 2020), and evaluating invader impacts on recipient communities is essential to assess risks and determine which species should be prioritized for invasive species management to prevent further spread and mitigate impacts (Pysek et al. 2020).

Here we demonstrate the utility of an invasion-regime framework to evaluate invader impacts that can be used across a broader range of systems that better captures the temporal dynamics of invasions.

References.

Aagaard K, Lockwood JL (2016) Severe and rapid population declines in exotic birds. Biological Invasions 18:1667–1678

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance–impact relationship for invasive species. Proceedings of the National Academy of Sciences 116:9919–9924

Castro-Díez P, Pauchard A, Traveset A, Vilà M (2016) Linking the impacts of plant invasion on community functional structure and ecosystem properties. Journal of vegetation science: official organ of the International Association for Vegetation Science 27:1233–1242

Catford JA, Bode M, Tilman D (2018) Introduced species that overcome life history tradeoffs can cause native extinctions. Nature Communications 9:2131

Chambers JC, Brown JL, Bradford JB, Board DI, Campbell SB, Clause KJ, Hanberry B, Schlaepfer DR, Urza AK (2023) New indicators of ecological resilience and invasion resistance to support prioritization and management in the sagebrush biome, United States. Frontiers in Ecology and Evolution 10:1009268

Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366

Crystal-Ornelas R, Lockwood JL (2020) The 'known unknowns' of invasive species impact measurement. Biological Invasions 22:1513–1525

D'Antonio, C., Levine, J. and Thomsen, M. (2001) Ecosystem Resistance to Invasion and the Role of Propagule Supply: A California Perspective. Journal of Mediterranean Ecology, 2, 233-246.

D'Antonio CM, Vitousek PM (1992) Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. Annual Review of Ecology and Systematics 23:63–87

Denley D, Metaxas A, Fennel K (2019) Community composition influences the population growth and ecological impact of invasive species in response to climate change. Oecologia 189:537–548

Fenesi A, Botta-Dukát Z, Miholcsa Z, Szigeti V, Molnár C, Sándor D, Szabó A, Kuhn T, Kovács-Hostyánszki A (2023) No consistencies in abundance–impact relationships across herbaceous invasive species and ecological impact metrics. Journal of Ecology 111:1120–1138

Gaertner M, Biggs R, Te Beest M, Hui C, Molofsky J, Richardson DM (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships.

Diversity & Distributions 20:733–744

Gaertner M, Holmes PM, Richardson DM (2012) Biological invasions, resilience and restoration. Restoration ecology: the new frontier 265–280

Hallett LM, Hsu JS, Cleland EE, Collins SL, Dickson TL, Farrer EC, Gherardi LA, Gross KL, Hobbs RJ, Turnbull L, Suding KN (2014) Biotic mechanisms of community stability shift along a precipitation gradient. Ecology 95:1693–1700

Hobbie SE (2015) Plant species effects on nutrient cycling: revisiting litter feedbacks. Trends in Ecology & Evolution 30:357–363

Hulton VanTassel HL, Hansen AM, Barrows CW, Latif Q, Simon MW, Anderson KE (2014) Declines in a ground-dwelling arthropod community during an invasion by Sahara mustard (Brassica tournefortii) in aeolian sand habitats. Biological Invasions 16:1675–1687

Kalisz S, Kivlin SN, Bialic-Murphy L (2021) Allelopathy is pervasive in invasive plants. Biological Invasions 23:367–371

Letten AD, Dhami MK, Ke P-J, Fukami T (2018) Species coexistence through simultaneous fluctuation-dependent mechanisms. Proceedings of the National Academy of Sciences of the United States of America 115:6745–6750

Levine JM, Rees M (2002) Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. The American Naturalist 160:452–467

Lonsdale, W.M. (1999), Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

Loreau M (2010) From Populations to Ecosystems. Princeton University Press

Loreau M, de Mazancourt C (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. The American Naturalist 172:48–66

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13:195–198

Mangla S, Callaway RM (2007) Exotic invasive plant accumulates native soil pathogens which inhibit native plants. Journal of Ecology 96:58-67

Marushia RG, Cadotte MW, Holt JS (2010) Phenology as a basis for management of exotic annual plants in desert invasions. Journal of Applied Ecology 47:1290–1299

Miller AD, Inamine H, Buckling A, Roxburgh SH, Shea K (2021) How disturbance history alters invasion success: biotic legacies and regime change. Ecology Letters 24:687–697

Ortega YK, Pearson DE (2005) Weak vs. Strong invaders of natural plant communities: Assessing invasibility and impact. Ecological Applications 15:651–661

Panetta FD, O'Loughlin LS, Gooden B (2019) Identifying thresholds and ceilings in plant community recovery for optimal management of widespread weeds. NeoBiota 42:1–18

Pearse IS, Sofaer HR, Zaya DN, Spyreas G (2019) Non-native plants have greater impacts because of differing per-capita effects and nonlinear abundance-impact curves. Ecology Letters 22:1214–1220

Pendergrass AG, Knutti R, Lehner F, Deser C, Sanderson BM (2017) Precipitation variability increases in a warmer climate. Scientific Reports 7:17966

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological reviews of the Cambridge Philosophical Society 95:1511–1534

Qu T, Du X, Peng Y, Guo W, Zhao C, Losapio G (2021) Invasive species allelopathy decreases plant growth and soil microbial activity. PloS One 16:e0246685

Ryo M, Aguilar-Trigueros CA, Pinek L, Muller LAH, Rillig MC (2019) Basic Principles of Temporal Dynamics. Trends in Ecology & Evolution 34:723–733

Sanders A, Minnich R (2000) Brassica tournefortii. Invasive plants of California's wildlands. University of California Press, Berkeley, CA

Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220

Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. Ecosphere 9:e02415

Strayer DL, D'Antonio CM, Essl F, Fowler MS, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pyšek P, Robertson P, von Schmalensee M, Stefansson RA, Wright J, Jeschke JM (2017) Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecology Letters 20:1337–1350

Spasojevic MJ, Catano CP, LaManna JA, Myers JA (2018) Integrating species traits into species pools. Ecology 99:1265–1276

Valencia E, de Bello F, Galland T, Adler PB, Lepš J, E-Vojtkó A, van Klink R, Carmona CP, Danihelka J, Dengler J, Eldridge DJ, Estiarte M, García-González R, Garnier E, Gómez-García D, Harrison SP, Herben T, Ibáñez R, Jentsch A, Juergens N, Kertész M, Klumpp K, Louault F, Marrs RH, Ogaya R, Ónodi G, Pakeman RJ, Pardo I, Pärtel M, Peco B, Peñuelas J, Pywell RF, Rueda M, Schmidt W, Schmiedel U, Schuetz M, Skálová H, Šmilauer P, Šmilauerová M, Smit C, Song M, Stock M, Val J, Vandvik V, Ward D, Wesche K, Wiser SK, Woodcock BA, Young TP, Yu F-H, Zobel M, Götzenberger L (2020) Synchrony matters more than species richness in plant community stability at a global scale. Proceedings of the National Academy of Sciences 117:24345–24351

Valone TJ, Balaban-Feld J (2018) Impact of exotic invasion on the temporal stability of natural annual plant communities. Oikos 127:56–62

Valone TJ, Weyers DP (2019) Invasion intensity influences scale-dependent effects of an exotic species on native plant diversity. Scientific Reports 9:18769

Vetter VMS, Kreyling J, Dengler J, Apostolova I, Arfin-Khan MAS, Berauer BJ, Berwaers S, De Boeck HJ, Nijs I, Schuchardt MA, Sopotlieva D, von Gillhausen P, Wilfahrt PA, Zimmermann M, Jentsch A (2020) Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought. Global Change Biology 26:3539–3551

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702–708

Weidlich EWA, Flórido FG, Sorrini TB, Brancalion PHS (2020a) Controlling invasive plant species in ecological restoration: A global review. Journal of Applied Ecology 57:1806–1817

Yelenik SG, D'Antonio CM (2013) Self-reinforcing impacts of plant invasions change over time. Nature 503:517–520

Allen M, Rotenberry J, Scott T (2005) Coachella Valley Multiple Species Habitat Conservation Plan Monitoring Program. Coachella Valley Association of Governments-County of Riverside.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, ''Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Braak C, Weedon J (2022). _vegan: Community Ecology Package_. R package version 2.6-2, <https://CRAN.R-project.org/package=vegan>.

Wagg C, Roscher C, Weigelt A, Vogel A, Ebeling A, de Luca E, Roeder A, Kleinspehn C, Temperton VM, Meyer ST, Scherer-Lorenzen M, Buchmann N, Fischer M, Weisser WW, Eisenhauer N, Schmid B (2022) Biodiversity–stability relationships strengthen over time in a long-term grassland experiment. Nature communications 13:1–11
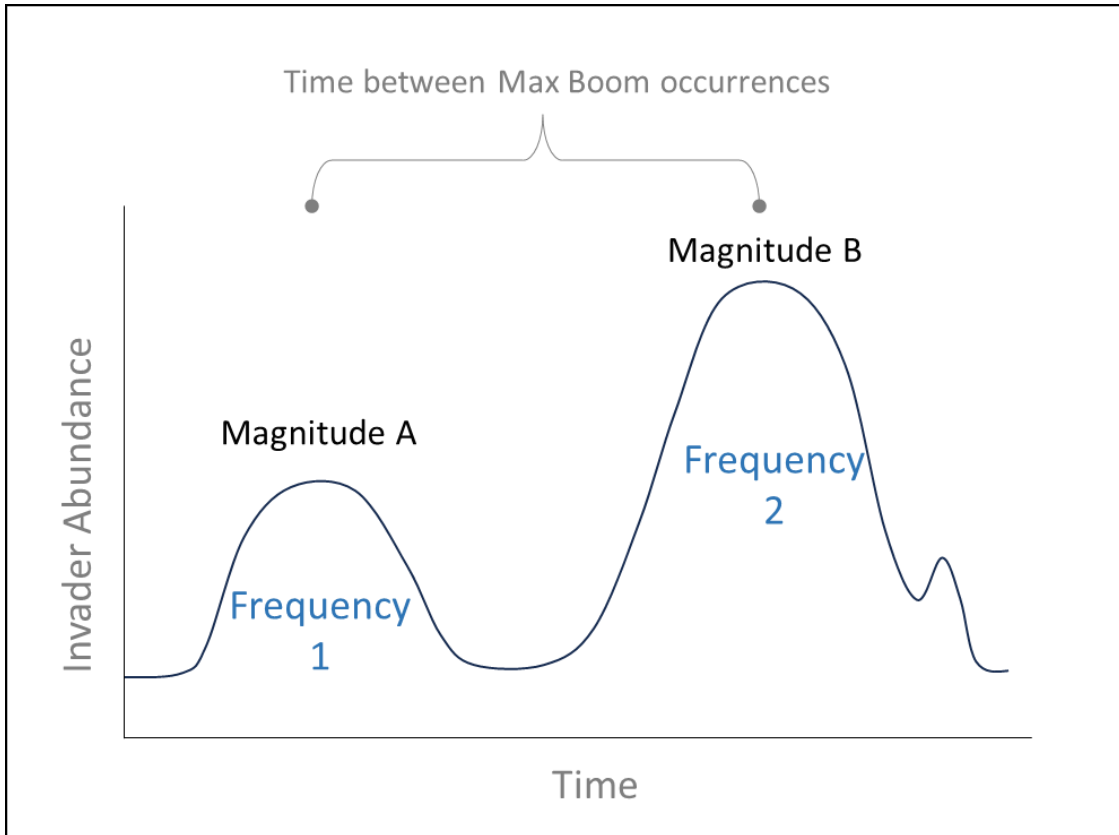
Figure 1. Conceptual figure of attributes of an invasion regime for a system that experiencing cyclical boom dynamics. Boom frequency refers to the number of boom events that occur during the study period. Boom magnitude refers to the max abundance of the invader in comparison to baseline native vegetation in the absence of invaders. Type B booms are the strongest magnitude, with invader abundance exceeding the native baseline abundance. Type A booms are of lower magnitude, with invader abundances reaching half the native baseline abundance. Mean return interval of boom occurrences is taken by calculating the average of time between max boom occurrences.
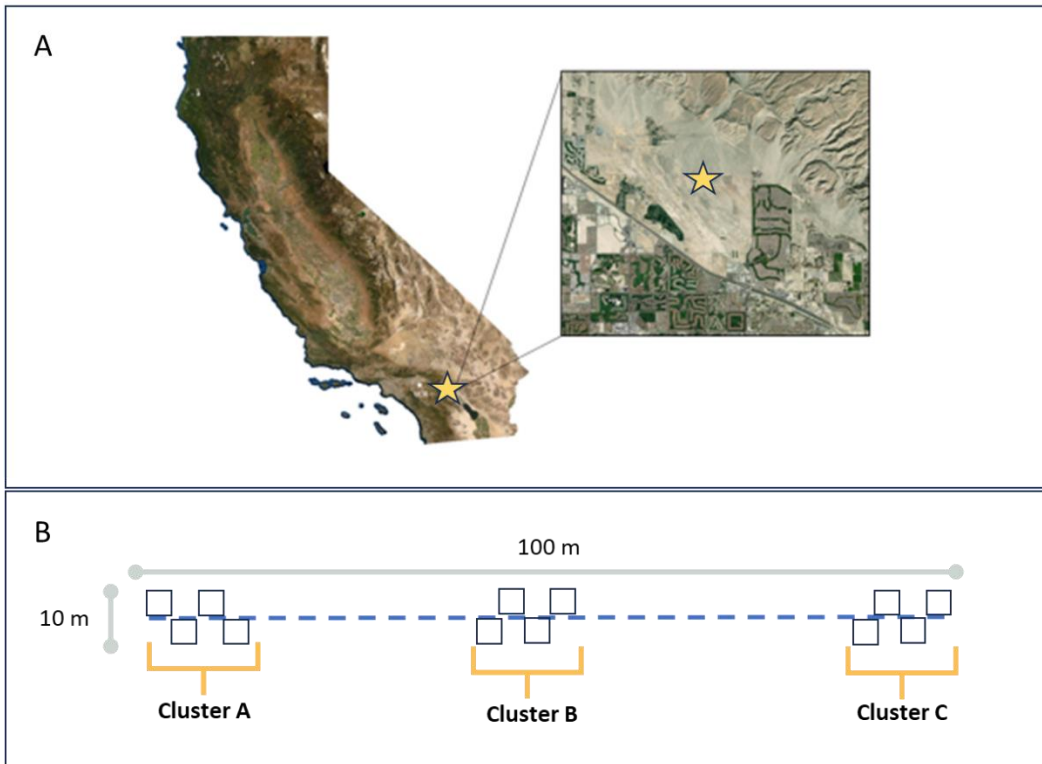
Figure 2. A) Study Site location, Coachella Valley, CA, USA. B) Study design of 0.1 ha belt transects showing the spatial arrangement of 1m^2 quadrats placed within clusters used to collect vegetative data.
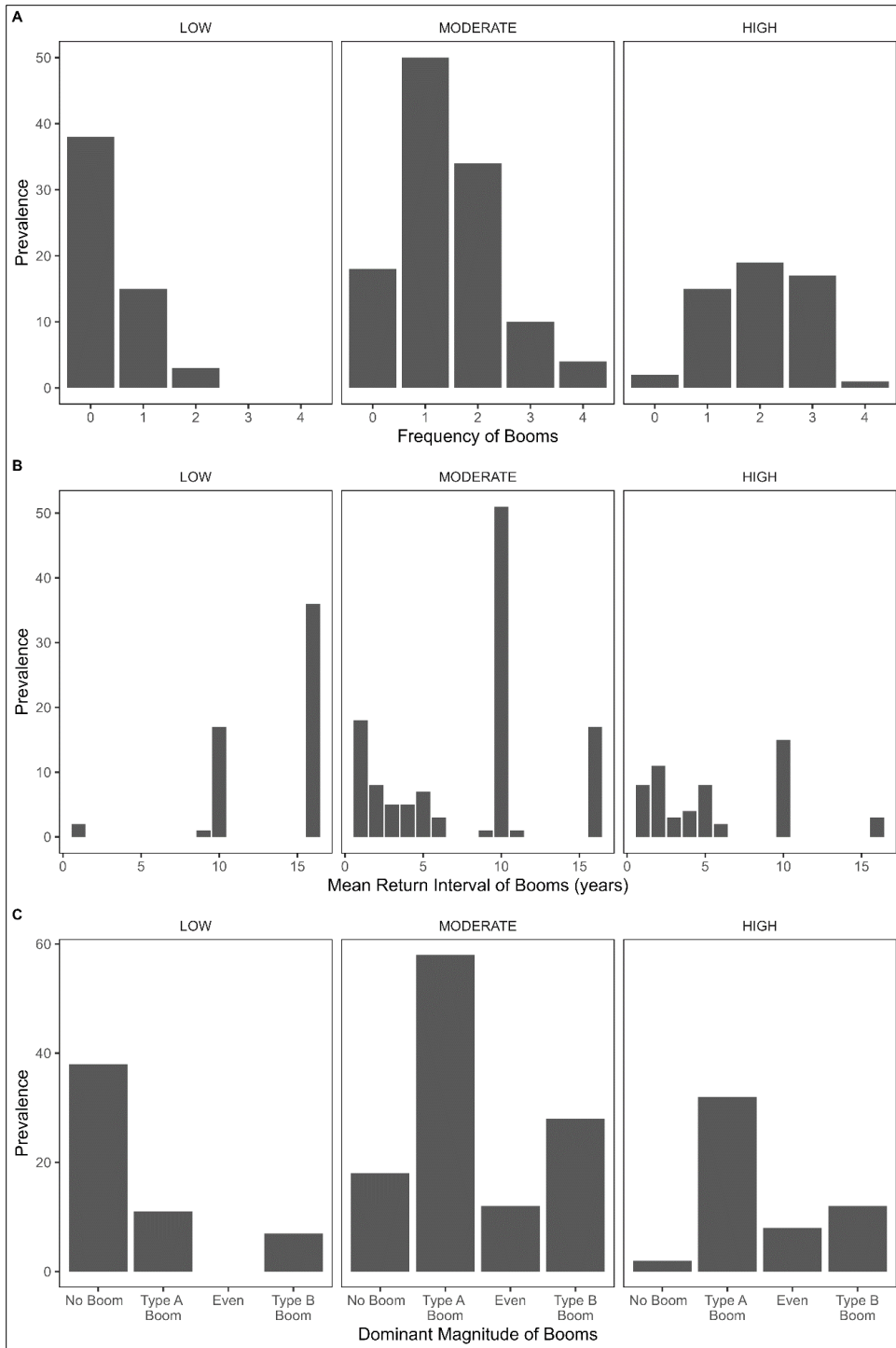
Figure 3. Underlying invasion level mediates the dynamics experienced in a community. Histograms showing the prevalence of invasion regime attributes, A) frequency of booms B) mean return interval of booms, and C) dominant magnitude of booms by invasion level.

Table 1. Summary of Pearson's Chi Squared X^2 testing independence between invasion regime attributes.

	Invasion Level									
	LOW $N= 56$		MODERATE $N= 116$		HIGH $N= 54$		TOTAL $N= 226$		X^2	df	p-value
	n	$\%$	n	$\%$	n	$\%$	n	$\%$			
Frequency of Booms									96.583	8	**<0.001**
0	38	67.85	18	15.52	2	3.7	58	25.66			
1	15	26.79	50	43.1	15	27.78	80	35.39			
2	3	5.36	34	29.31	19	35.19	56	24.78			
3	0	0	10	8.62	17	31.48	27	11.95			
4	0	0	4	3.45	1	1.85	5	2.21			
Mean Return interval of Booms									90.144	8	**<0.001**
1	2	3.57	18	15.52	8	14.81	28	12.39			
2	0	0	8	6.91	11	20.37	19	8.41			
3	0	0	5	4.31	3	5.56	8	3.54			
4	0	0	5	4.31	4	7.41	9	3.98			
5	0	0	7	6.03	8	14.81	15	6.64			
6	0	0	3	2.59	2	3.7	5	2.21			
7	0	0	0	0	0	0	0	0			
8	0	0	0	0	0	0	0	0			
9	1	1.79	1	0.86	0	0	2	0.88			
*10	17	30.36	51	43.97	15	27.78	83	36.73			
11	0	0	1	0.86	0	0	1	0.44			
12	0	0	0	0	0	0	0	0			
13	0	0	0	0	0	0	0	0			
14	0	0	0	0	0	0	0	0			
15	0	0	0	0	0	0	0	0			
*16	36	64.29	17	14.66	3	5.56	56	24.78			

Dominant Magnitude of Booms								74.755	6	<0.001
No Boom	38	67.86	18	15.52	2	3.7	58	25.66		
Type A boom	11	19.64	58	50	32	59.26	101	44.69		
Even	0	0	12	10.34	8	14.81	20	8.85		
Type B Boom	7	12.5	28	24.14	12	22.22	47	20.79		
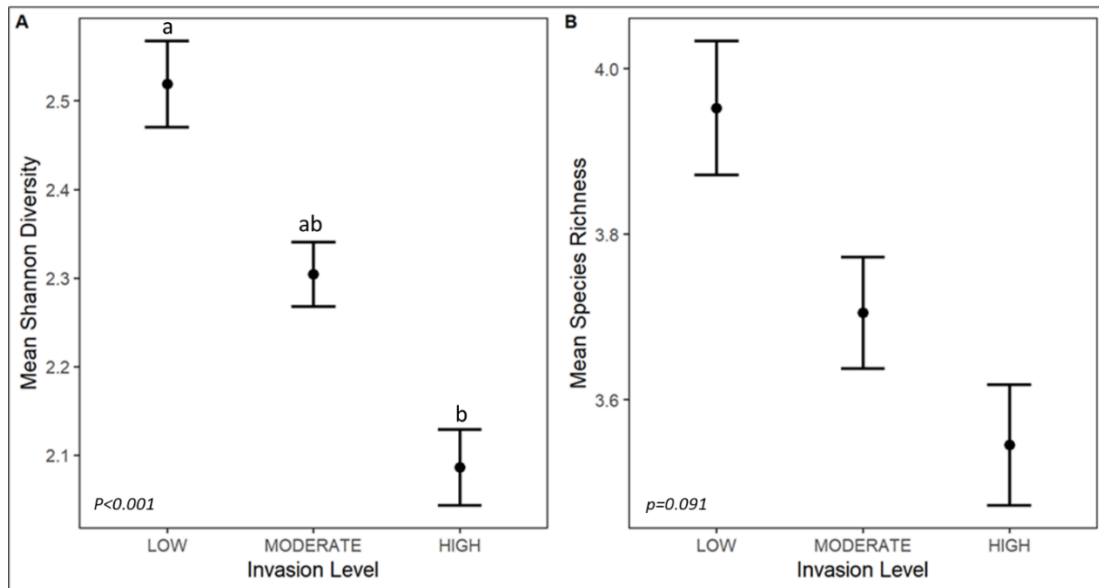
Figure 4. Mean study extent (2003-2019) A) Shannon Diversity and B) species richness by invasion level. Error Bars represent 1 SE. Letters denote statistical differences <0.05.

Table 2. Summary model statistics for Analysis of variance (ANOVA) of Shannon diversity, and species richness values as function of invasion level. Bolded p values indicate significance < 0.05.

	Shannon Diversity			*Species Richness*		
Predictors	**DF**Num, Den	**F value**	***p* value**	**DF**Num, Den	**F value**	***p* value**
Invasion level	2,54	9.170	**<0.001**	2,54	2.501	0.091
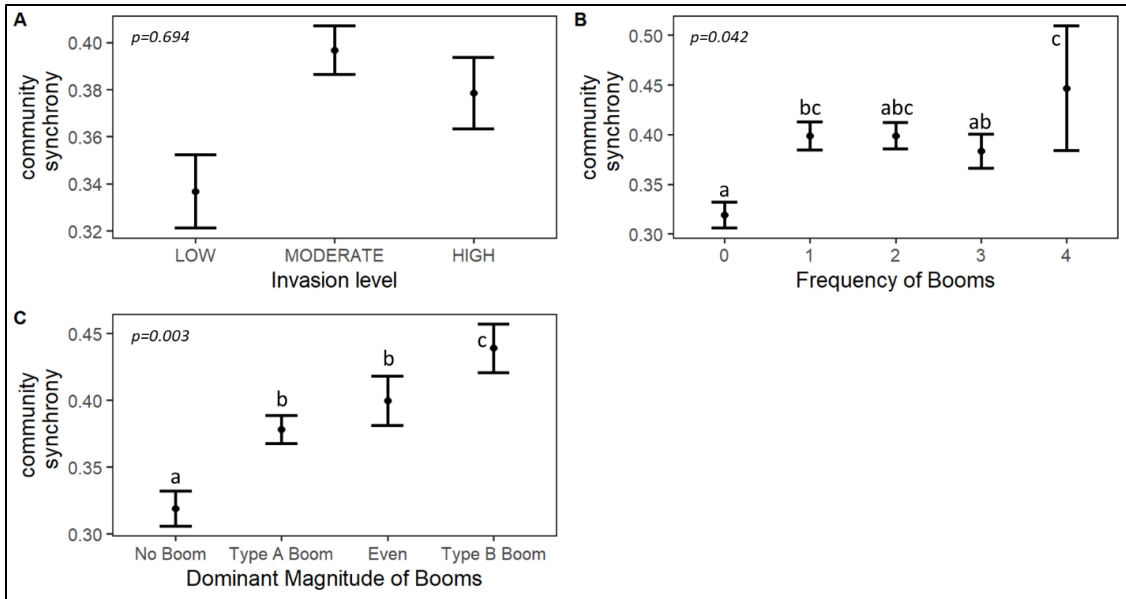
Figure 5. Community synchrony as a function of A) invasion level, B) frequency of booms, and C) dominant magnitude of booms. Letters denote significant differences <0.05.
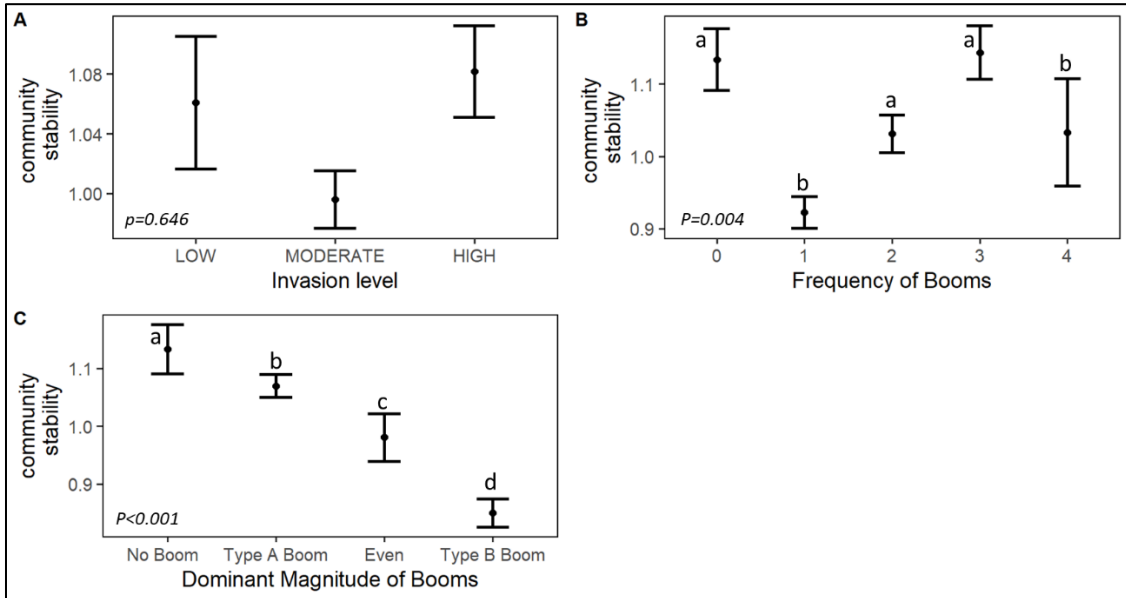
Figure 6. Community stability as a function of A) invasion level, B) frequency of booms, and C) dominant magnitude of booms. Letters denote statistical differences <0.05.

Table 3. Summary model statistics for Analysis of variance (ANOVA) of community synchrony and community stability as function of invasion level, frequency of booms, dominant magnitude of booms, and their interactions. Bolded p values indicate significance < 0.05.

Predictors	Community synchrony			Community stability		
	$DF_{Num, Den}$	F value	*p* value	$DF_{Num, Den}$	F value	*p* value
Invasion level	2,108	0.365	0.695	2,115	0.438	0.646
Frequency of Booms	4,188	3.765	**0.005**	4,192	7.772	**<0.001**
Dominant Magnitude of Booms	2,182	5.869	**0.003**	2,186	9.859	**<0.001**
Invasion level: Frequency of Booms	6,187	1.373	0.228	6,191	1.053	0.393
Invasion level: Dominant Magnitude of Booms	3,187	1.373	0.263	3,191	0.914	0.435
Frequency of Booms: Dominant Magnitude of Booms	3,180	1.962	0.121	3,185	0.385	0.764
Invasion level: Frequency of Booms: Dominant Magnitude of Booms	2,187	0.854	0.427	2,192	1.642	0.196
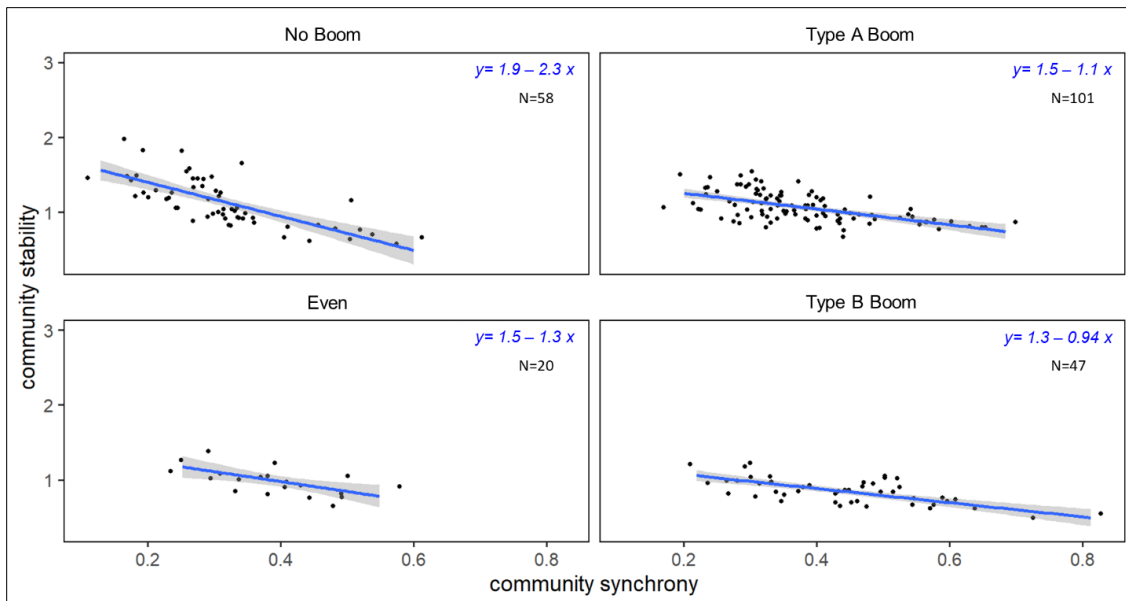
Figure 7. Community stability by community synchrony and dominant magnitude of booms. Each dot represents a study plot. Grey shading indicates SE of linear relationship.

Table 4. Summary model statistics for Analysis of Variance (ANOVA) of community stability as function of community synchrony, dominant magnitude of booms, and their interactions. Bolded p values indicate significance < 0.05.

	Community stability		
Predictors	**DF**$_{\text{Num, Den}}$	**F value**	***p* value**
Community Synchrony	1,215	92.309	**<0.001**
Dominant Magnitude of Booms	3,217	7.280	**<0.001**
Community Synchrony: Dominant Magnitude of Booms	3,217	6.776	**<0.001**

Chapter 3

Efficacy of invasive plant control depends on season of herbicide application and

invader soil seedbank density

Abstract. Understanding the underlying temporal dynamics influencing invasive plant control outcomes is essential to achieve restoration and land management goals. Within grasslands, herbicides are commonly used as the main method for invasive plant control, but the efficacy of management may be dependent on seasonal dynamics, as well as the number of applications. Additionally, assessments to quantify invasive plant control are often limited to aboveground plant composition, overlooking the potential repository of propagules stored in the soil seedbank, and additional impacts on non-target species. To ensure that an herbicide method is effectively controlling invader populations, while limiting impacts on the resident plant communities, both above and belowground species responses must be assessed. We established herbicide field experiments across different sites and years in Riverside, CA, USA, to assess the control of a global annual invasive forb, *Oncosiphon pilulifer*. We investigated how seasonal herbicide management (Fall vs Spring) and repeated annual herbicide applications (one vs two years) influenced cover and seedbank density of our focal invader and the resident plant community one year after treatment. We found that although spring and fall-applied herbicides reduced invader cover, fall applications were the only strategy to provide long-term management

by reducing the focal invader's seedbank density in the soil. Lastly, native cover was limited in post-treated areas, suggesting that additional management strategies may be needed to overcome native establishment limitations in invaded grasslands.

Introduction. Integrated invasive plant management is essential for carrying out effective restoration and land management. Costs for managing invasive species globally have tripled every decade and are expected to continue to increase, with a mean cost of $26.8 billion per year (Diagne et al. 2021). Part of the increasing cost is due to the variability in outcomes for management actions (Brudvig et al. 2017), as well as a lack of understanding of potential outcomes associated with invasion management strategies (Kettenring & Adams 2011). Certain strategies that effectively reduce the invader population may also unintentionally reduce native species within the managed communities, creating trade-offs of achieving one restoration goal (e.g., reduced invasive plant cover) at the cost of another goal (e.g., native recovery, maintaining or improving habitat for wildlife) during restoration efforts (Skurski et al. 2013). These tradeoffs may be manifested in the soil seedbank such that if soil seedbanks contain a large amount of invasive seed or are depleted of native seed, management goals may not be achieved (Gioria et al. 2014; Schwartz-Lazaro & Copes, 2019; Silva & Overbeck, 2020). Yet, seedbanks are often overlooked when evaluating land management techniques (Kiss et al. 2018; Larson & Suding, 2022). Thus, enhancing the success of restoration goals requires identification of suitable integrated invasive plant management strategies that reduce or eradicate invader populations, while limiting unintended impacts on the native community (Roiloa et al. 2020), and should include assessments of soil seedbanks.

Improving the ability to control invasive plant populations is contingent on deciphering how temporal dynamics may influence herbicide management efficacy (Kyser et al. 2011; Ziska, 2016). One consideration is how the seasonality of herbicide

application may impact invader control (i.e., reduce invader abundance). For example, post-emergent herbicides (e.g., glyphosate) are applied throughout the growing season to prevent seed production, while pre-emergent herbicides (e.g., indaziflam) are applied directly to the soil prior to the start of the growing season, and are activated by rainfall or irrigation, preventing seedling establishment. The outcome of the seasonal timing of herbicide application can be dependent on the target invader and its demographic stage at time of management (Bahm et al. 2011; Weidlich et al. 2020). For instance, Kyser et al. 2011 found that controlling invasive Yellow Starthistle (*Centaurea solstitalis*) was more effective when herbicides were applied at the seedling stage (winter) compared to when herbicides were applied before the growing season (fall) or during the rosette stage (spring). Conversely, Rohal et al. 2019 found that herbicides sprayed in the fall resulted in less invasive common reed (*Phragmites australis*) cover due to the rhizome being killed early on before the growing season started, compared to when actively growing plants were sprayed during the summer. The number of herbicide applications required to reduce the growth and spread of invasive species may also vary depending on the species and active ingredient of the selected herbicide (Gaskin et al. 2021). While some herbicides provide temporary relief in controlling invasions after one application, repeated applications are often necessary to prevent or reduce the rate of re-colonization from other non-native species surrounding the community (i.e., secondary invasion, Pearson et al. 2016), or prevent re-colonization of the focal invader (i.e., reinvasion, Lazarus & Germino, 2022), highlighting the struggles that can arise when actively managing aggressive invasions. To maximize efficacy of management strategies,

experimental studies must therefore include elements that capture the multiple temporal

dimensions (e.g., timing of application, number of applications) that mediate invasive

plant management.

Equally important is the role that soil seedbanks play in invasion dynamics by

providing a reservoir for dormant seeds to persist in the soil when conditions

aboveground are unfavorable. Effective treatments may therefore be dependent on the

seedbanking strategy of the invader (Gioria & Osborne, 2014). For instance, depleting the

invader seedbank with repeated herbicide applications may be more feasible for species

with transient seedbanks, such as non-native annual grasses, some of which produce

seeds that can remain viable in the soil for up to 18 months (Jurand et al. 2013).

Alternatively, it may be more difficult to exhaust the soil seedbank of an invader that has

a persistent seedbank where seeds can remain viable in the soil for 2-5 years, or

sometimes even longer (Gioria & Pysek, 2015). Managing invader seedbanks is further

complicated by species that produce many propagules or by the length of invasion at the

site, which can result in a soil seedbank that is dominated by invasive seeds, making

treatments less effective at managing invader populations long-term (Schwartz-Lazaro &

Copes, 2019; Larios et al. 2013). Hence, studies evaluating invasive plant management

strategies may be improved by including assessments on the invader seedbank (e.g., seed

density, seed viability), in addition to aboveground cover assessments (A.H. et al. 2022).

Lastly, it's important to consider that managing invasive plants can

unintentionally affect other species within the community that are not the primary focus

of management efforts (i.e., native and resident species) but are still vulnerable to

treatment impacts (hereafter, *non-target species*). Common invasive plant management

treatments such as mowing, herbicides, and flooding have proven to effectively reduce

invader cover; however, these strategies can also result in a reduction of native

abundance and diversity (Kettering & Adams, 2011; Weidlich et al. 2020). Native plant

recovery trajectories after management treatments can be dependent on a variety of site

factors, such as environmental variability (Dickens et al. 2015; Copeland et al. 2019) or

secondary invasions (Pearson et al. 2016). Prior et al. 2018 found that out of 151 studies

where invasive species were removed using a variety of methods (e.g., mechanical,

manual, and chemical control) only 51% of invader removal sites resulted in a positive

outcome for native ecological recovery, while the remainder 49% resulted in sites with

negative or unintended consequences on native recovery. Additionally, native recovery

may be limited by management treatments interacting with invader legacies, especially in

areas where the residence time (i.e., time since introduction) of the invader is long

(Corbin & D'Antonio, 2012). In heavily invaded areas, such as California shrublands,

where the soil seedbank contains on average more non-native seeds per meter squared

compared to native seeds (Cox & Allen, 2008), herbicides may cause a reduction in the

already depleted native seedbank, compromising future plant recruitment (Flory and

Clay, 2009). To prevent unintended impacts on native recovery, treatment assessments

must also include responses of non-target species, in addition to invader responses, within

the managed community.

  Within California grasslands and shrublands, the management of a relatively new

invader, *Oncosiphon pilulifer*, (hereafter, *stinknet*) provides an excellent opportunity to

explore these various dynamics in invaded grasslands. Stinknet is an annual winter forb native to South Africa that is invading regions of North America and Australia, with sparse observations in Asia and Europe (GBIF.org, DOI10.15468/dl.wb85ub). This invader creates dense stands and is expanding its introduced range rapidly, having spread over 1,000 km across southwestern North America in 40 years. During the early growing season, it can be challenging to detect and treat due to faster-growing, non-native species making stinknet seedlings inconspicuous. Stinknet produces inflorescences that average 3,000-5,000 seeds per plant, with a seedbank that is persistent for 5 years (Douglas & Nicholson 2019). Stinknet has been identified as one of the top 5 invasive species in Western Australia at risk of increasing in severity with climate change (Michael et al. 2011). Consequently, management recommendations were issued to focus on containing the spread of stinknet to prevent further range expansion and impacts of this species. There is some evidence of effective control methods (Hedrick and McDonald 2020); however, those studies did not explore how treatments influence the seedbank or non-target species. Additionally, in this invaded grassland system, the long-term presence of other plant invaders has been documented to deplete or inhibit the germination of the native seedbank, reducing the potential for recruitment post-management (Cox & Allen, 2008; Gioria & Pysek, 2015; Gioria et al. 2021). This system also consists of many California native annual species with long-lived seeds that utilize the seedbank to overcome climate variability, suggesting that aboveground vegetation may not always be representative of the seedbank community at a given time (LaForgia et al. 2018). This seedbanking strategy may leave the long-lived native seeds in the soil vulnerable to non-

97

target impacts from chemical treatments. Further, annual grasslands in California experience high species turnover and temporal variability (Hobbs and Mooney 1995; Cleland et al. 2013; Harrison et al. 2020), making it difficult to find a consistent management strategy to control the invasive species, while limiting impacts on the native community.

To improve our understanding of how underlying temporal dynamics influence above and belowground species responses during invasive plant control, we established a field experiment, across three different sites, assessing the control of stinknet. We asked for all plots one year after treatment: (1) How does seasonal herbicide management (Fall vs. Spring) and repeated annual herbicide applications (one vs. two years) influence stinknet cover?, 2) How does seasonal herbicide management and the number of annual herbicide applications influence stinknet density in the soil seedbank?, (3) How does seasonal herbicide management and the number of herbicide applications influence non-target species both aboveground and in seedbank communities?

Methods. <u>Study Sites.</u> We conducted herbicide field experiments at three invaded grassland sites within Riverside County, California, U.S.A: Lake Matthews Estelle Mountain Reserve (33°5''11.'''''N, 117°2''56.'''''W), Lake Perris State Recreation Area (33°5''17.'''''N, 117°0''47.'''''W) and Motte Rimrock Reserve (33°43'5.6'' N, 117° 15'37.98'' W) from 2018 to 2021 (Fig 1A). Riverside County is believed to be the geographical area where stinknet was first introduced into North America before expanding its range into the Southwestern United States (Hedrick & McDonald, 2020). Study sites experience a Mediterranean-type climate, as summers are hot and dry while

winters are cool and wet (see Table S1 for annual temperatures and precipitation). All three sites contain native forbs (e.g., *Amsinckia menziesii*, *Croton setigerus*, *Deinandra fasciculata*) but are dominated by non-native invasive annual grasses (e.g., *Bromus rubens*, *Bromus diandrus*, *Hordeum murinum*, *Avena fatua*, *Avena barbata*, *Schismus barbatus*) and non-native invasive forbs (*Oncosiphon pilulifer*, *Erodium cicutarium*, *Brassica nigra*). Species nomenclature follows the Jepson (Jepson Flora Project, 2023).

Experimental Design. We set up two subblocks at each site, with 16 (2 x 5 m) herbicide treatment plots, spaced 1.5 m apart, arranged in a 4 x 4 grid per subblock (n=32 plots per site) (Fig. 1B). To test the effect of seasonal herbicide management (Fall vs. Spring) and repeated annual herbicide applications (one vs. two years), we used a split-plot design with a nested factorial experiment. The main plot effect was one vs two years of herbicide application which was assigned to one of the two subblocks. The 16 plots were assigned to a factorial experiment of seasonal herbicide management, where we used three different herbicides for each the fall and spring application strategies (fall: aminopyralid, indaziflam, isoxaben+dithiopyr; spring: glyphosate, clopyralid, triclopyr). We replicated different herbicides versus a single herbicide to estimate the overall effect of an herbicide strategy. We randomly assigned one of the six treatments to a plot with two control plots that received no herbicide application, and were used to estimate the baseline cover of stinknet within untreated vegetation (n=8). The remaining eight plots within a block were randomly assigned to the same treatments but served as a replicate over time (2018 vs. 2019). We replicated this design across our three sites for a total of 96 plots (Fig. 1). One subblock within each site was sprayed only once during the

assigned season (Fall or Spring) with no second-year treatment, while another block was sprayed once during the assigned season (Fall or Spring), two years in a row. Due to COVID research restrictions, we were unable to apply the second round of herbicides during the 2020 Fall season. This affected 9 plots (3 plots at each site). The results we present are therefore a conservative estimate of the effects of two applications.

Herbicides were applied using an 80-inch spray boom for one continuous broadcast spray (see Table S2 for concentrations used) across the entire 2 x 5 m experimental plot. Each plot assigned with a fall-applied herbicide was sprayed directly onto the soil surface and over any existing dead plant vegetation that remained in the plot in November. Using historical rainfall data, November was selected to ensure that at least a 6mm rain event occurred within a month of application to activate the herbicides. For the spring-applied treatment, the herbicide was sprayed on all actively growing plants present within the 2 x 5 m plot. The timing of spring herbicide application was dependent on the phenology of stinknet, as we sprayed in either March or April when stinknet was starting to bud and <5% of the population was flowering (see Table S3 for dates).

Plant Sampling. To assess how the herbicides impacted the plant community, we established a 1 m² subplot that was representative of the vegetative community present within the larger 2 x 5 m (Fig 1C). Within this subplot, we made visual estimates of aboveground plant cover for each species, total litter, and bare ground cover. We classified litter as any dead vegetative growth from the previous year. We classified bare ground as the total amount of plot covered by barren soil. Species that were present as single individuals were recorded as 0.25 % cover. Because of the overlapping canopy

100

cover of plant species and litter, total cover in a subplot could be over 100 %. Species that were not present in the meter squared plot but were present within the larger 2 x 5 m experimental plot were recorded for richness measures. We took aboveground community composition measurements in the spring during peak biomass, one year after treatment.

Seedbank Sampling. To assess soil seedbank responses, we collected three soil cores, measuring 2.5 cm in diameter, taken from the top 5 cm of the soil, from each treatment plot across our sites (96 plots * 3 cores/plot= 288 cores). We aggregated the three soil cores per treatment plot into one sample per treatment plot (n=96). Due to limitations caused by the COVID-19 pandemic, we were unable to collect soils one year after treatment. Instead, all soils were collected during July 2021 (2018 treated plots: Three years after treatment; 2019 treated plots: Two years after treatment). As a result of the delayed soil collection, our soil samples likely contained an extra year of propagules. Accordingly, any legacy effects of herbicide applications on germination may also have been minimized due to our delayed sampling.

To determine seedbank density, composition, and diversity, we conducted a seven-month seedling emergence trial in a greenhouse from October 2021-April 2022. To maximize the emergence of seeds stored in the seedbank during our trial, we subsetted our aggregated soil samples that were taken from our experimental plots (n=96) into three 25.4cm x 25.4cm flats (n=288). Each of the trays was assigned with one of the following germination sub-treatments: 1) water saturation, where we watered every tray to saturation for the first two weeks of the trial, 2) cold stratification, where we placed the

soil samples in a 4°C refrigerator for two weeks prior to the start of the trial, and 3) ambient, which received periodic watering throughout the seedbank study but was not subjected to soaking or cold stratification. Flats were watered by automated misters every other day for 15 minutes a day. We recorded species identity and number of seedlings that emerged in each tray on a weekly basis throughout the study. Once we identified seedlings, they were recorded and discarded to prevent double counting. To determine a positive species identification, representative seedlings were transplanted for each species in a separate tray and grown until flowering. Seedling densities from each of the three sub-treatments were summed up at the end of the emergence trial to give an estimate of total viable seeds and species present per experimental plot.

Analyses. To assess herbicide responses of our focal invader, we conducted a linear mixed effect model with season managed (fall, spring, control), number of herbicide applications (one, two), and their interactions as fixed effects. Since the vegetative community can vary from one year to the next, as well as from one site to the next, we included two random factor terms: year surveyed nested within site, and initial year of treatment as the second factor. We used this model structure for the aboveground analysis, with percent cover of stinknet per meter squared as the response variable, and again used this model for our seedbank analysis, with stinknet seed density per meter squared as the response variable. To evaluate the effectiveness of a particular herbicide within a seasonal strategy, we ran two separate models with a reduced data set. One model evaluated herbicide treatments that were sprayed in the spring, and a separate model evaluated the herbicide treatments that were sprayed only in the fall. Within each

of these models, we chose active ingredient of herbicide treatment, number of herbicide applications, and their interactions as fixed effects, along with the same random factor terms used in our other models. Stinknet cover or seed density were used as the response variables. We used Tukey's post-hoc tests to compare individual levels of treatment in our models.

To test if aboveground plant community composition differed among treatments, we conducted a permutational analysis of variance (PERMANOVA, Anderson, 2001) based on Bray–Curtis dissimilarity matrices using the adonis() function from the 'vegan' package (Oksanen et al. 2020), and visualized results using nonmetric multidimensional scaling (NMDS). We included the species composition of all the plots per herbicide management strategy (fall, spring, control) across our sites and used the herbicide strategy and number of repeated applications as our treatment groups. We ran 999 permutations, with site and year treated as a random factor. Since species cover is highly variable interannually, and across our study sites, we aggregated species cover into five cover category types as our response variable: litter, bare, native, non-native grasses, and non-native forb species, to avoid species-specific interactions from overshadowing the treatments.

To assess diversity responses, we first calculated the Shannon-Weiner Diversity Index for each of the aboveground and seedbank communities. We then conducted a linear mixed effects model with this diversity metric as the response variable, and the following as fixed factors: season managed (fall, spring, control), number of applications (one vs two), community type (aboveground vs. seedbank), and their interactions. Within

this model, we included block nested within site as our first random factor, and initial

year of treatement as the second random factor. We used Tukey's post-hoc tests to

compare individual levels of factors within our models. All statistical analyses were

conducted using R Statistical Software (version 4.1.2.; R Core Team, 2021). Models were

run using the 'LME4' package (Bates et al. 2015), and were checked and validated to

meet assumptions. Data were either log10 transformed (aboveground composition data)

or square root transformed plus a constant (seedbank germination data) to meet normality

assumptions.

Results. We detected 47 species (25 native and 22 non-native species) in our field and

greenhouse experiments across our study sites (See table S4 to view the full species list).

We observed that stinknet cover varied across years independent of our treatments (i.e.,

controls), where stinknet was most abundant during the 2018 growing season (control

average $49.45 \pm 12\%$ SE across sites, control range: 0-90%), compared to the 2019

$(32.61 \pm 5\%$SE, range: 0-95%), 2020 $(12.86 \pm 3\%$ SE, range: 0-80%) and 2021 $(4.1 \pm 1\%$

SE, range: 0-35%) growing seasons.

Q1: Herbicide management effects on stinknet aboveground cover

We found that one year after treatment, aboveground stinknet cover was strongly

influenced by the season of herbicide management (p<0.0001, Fig. 2A, Table S5), the

number of herbicide applications (p=0.0218), and an interaction between the two main

treatments (p=0.0150). With one application of herbicide, the fall-applied strategy

reduced stinknet cover by 100% compared to the spring-applied strategy and control plots

(post-hoc p<0.0001). The spring-applied strategy on the other hand did not differ from the control (spring=control, post-hoc p=0.9985). Within plots that received two years of application, the fall-applied strategy resulted in a reduction of stinknet cover compared to the spring strategy (post-hoc p=0.0029) and control (post-hoc p=0.0480). Although we observed slightly higher stinknet cover compared to the control treatment, the difference was not significant (post-hoc p=0.7977).

When we evaluated the effects of treatment within each seasonal strategy, we found that all individual fall-applied herbicides reduced stinknet cover to less than 5% which was significantly less cover compared to the control (post-hoc p<0.0010; Fig. 2B, Table S6). Individual spring-applied herbicides responses were more variable, as clopyralid was the only treatment that significantly reduced stinknet cover compared to the control (p=0.0326; Fig. 2C, Table S6).

Q2: Herbicide management effects on stinknet soil seedbank

The season of herbicide management influenced stinknet seed density in the seedbank, (p=0.0005; Fig. 3, Table S8). We found that fall-applied herbicides reduced stinknet seed density by 58% compared to the control (post-hoc p=0.0005, Fig. 3A, Table S8) and 62% compared to the spring-applied strategy (post-hoc p=0.0129). Although we saw a slight increase in seed density in the spring-applied plots compared to control plots, the difference was not significant (post-hoc p=0.2853). Stinknet seedbank density did not differ with the number of applications (p=0.8705) or with the interaction between treatments (p=0.5202).

When we evaluated stinknet seed densities within each seasonal management strategy, for the fall-applied treatments, we observed that the reduction in stinknet seed density in the soil was contingent on the active ingredient of the herbicide (p<0.0001, Fig. 3B, Table S8), with indaziflam plots being the only treatment that significantly reduced stinknet seed density compared to the control (Fig. 3B, post-hoc p<0.0001). Aminopyralid plots contained significantly lower seed density compared to the control treatments (p=0.0529) but higher seed densities compared to indaziflam (post-hoc p=0.0418). The isobaxen+dithiopyr herbicide mix on the other hand did not differ from the control (post-hoc p=0.4884). Stinknet seed densities were not affected by the number of applications (p=0.9294) or by an interaction between the two main treatments (p=0.9326). When we evaluated treatments applied within the spring season, we detected no difference in stinknet seed densities between the individual herbicide treatments (p=0.2802), number of applications (p=0.7350), or interactions between the two main factors(p=0.4054; Fig. 3C, Table S8).

Q3: Herbicide management impacts on non-target species in resident community

Aboveground composition

We found that one year after treatment, aboveground plant composition for non-target species significantly varied by season managed (PERMANOVA, R^2= 0.0745, p=0.0010), but not by the number of applications (PERMANOVA, R^2= 0.0167, p=0.0710) or the interaction between treatments (PERMANOVA, R^2= 0.0280, p=0.0810; Fig. 4, Table S9). Specifically, we found that the fall-applied strategy resulted in plots with a higher average of bare ground (14.4 $\pm$ 3.6%) and litter (43.9 $\pm$ 6%) cover

106

compared to the spring-applied (bare: $5 \pm 1.5\%$, litter: $24 \pm 4\%$) and control-treated plots (bare: $3.5 \pm 1.7\%$, litter: $31 \pm 4\%$). However, fall-applied strategy resulted in overall less non-native cover (forbs: $17.6 \pm 4.5\%$, grasses: $25.6 \pm 4\%$) compared to spring-applied (forbs: $35.2 \pm 4.6\%$, grasses: $30.5 \pm 5\%$) or control (forbs: $28.3 \pm 5.4\%$, grasses: $31 \pm 5.4\%$) strategies.

As for native cover, our data showed that native cover was significantly lower one year after treatment within fall-applied strategies (native: $3 \pm 1.1\%$) compared to the spring-applied (native: $9.5 \pm 1.8\%$) and control (native: $12 \pm 2.5\%$) strategies. We found no significant difference between community composition of spring-applied and control strategies (post-hoc $p=0.213$), as they were both dominated by non-native species, with small cover of native species, bare and litter cover.

Seedbank composition

Most seeds germinating during the seedling emergence experiment were from various non-native invasive species. The average seed density in the overall seedbank for our control plots was $7,505 \pm 993$ seeds/m² for all non-target, non-native invasive species, (not including our focal invader, stinknet) while the average seed density of total natives in the seedbank for our control plots was $4,697 \pm 753$ seeds/m² (Fig. 5). When we analyzed how management techniques influenced the density of non-native species in the seedbank (not including our focal invader, stinknet), we found no evidence to support that the season of herbicide management ($p = 0.4412$), the number of applications ($p=0.9857$), nor an interaction between the two factors ($p=0.1825$), significantly reduced seed density of non-target, non-native species in the soil seedbank. We found a similar

trend when we analyzed densities of native species within the soil seedbank, where

season managed (p=0.0693), the number of herbicide applications (p=0.4913), and the

interaction between factors (p=0.1624) had a weak influence on native seedbank density

(Table S11).

Aboveground vs Seedbank Diversity

Aboveground and seedbank plant communities varied by season managed

(p<0.0001, Fig.5, table S11). We found that fall-applied treatments contained on average

a Shannon diversity value of 2.89, which was significantly less compared to the spring-

applied strategy which contained an average Shannon diversity value of 3.37 (post-hoc

p=0.0276), and less compared to the control strategy which contained an average of 3.87

species per meter squared plot (post-hoc p<0.0001). Control plots had slightly higher

diversity compared to spring plots (p=0.0461). We also found that seedbank communities

consistently had higher Shannon diversity compared to aboveground plant communities

(p<0.0001, Fig. 5). Additionally, we found evidence for an interaction between the

number of applications and the composition of above vs seedbank communities

(p=0.0236, Fig. 5) influencing the diversity of species. Specifically, we found that

aboveground species diversity does not significantly vary between one or two

applications of herbicide (post-hoc p=0.6356), however seedbank species diversity

significantly decreases when plots receive two applications of herbicide (post-hoc

p=0.0179).

Discussion. Invasive plant management is a common part of site preparation and/or maintenance to assist recovery of native species during restoration projects (Wilson et al. 2011; Kimball et al. 2015). Herbicides are an important and frequently used tool in invasive plant management, yet variability in treatment efficacy and community responses post-treatment remain high. To identify strategies that are effective at controlling the invader population while limiting impacts on non-target species, we assessed the aboveground and soil seedbank composition responses of non-native and native species. We found evidence of multiple temporal dynamics influencing herbicide efficacy. For example, we observed that seasonal herbicide management strongly influenced invasive cover (Q1) and invasive seedbank density (Q2) yet only cover was impacted by multiple applications. We also found that aboveground cover of the resident non-target community was influenced by season managed, while the seedbank composition of non-target species was not influenced by the number of herbicide applications or season (Q3). Our study demonstrates that 1) efficacy of management is contingent on identifying key demographic stages and 2) recovery potential of native species is contingent on herbicide impacts on the resident community. Below we expand on these results in more detail.

Efficacy of invasive plant management treatment is contingent on identifying key demographic stages

Demographic approaches to management have been integral to conservation biology and are beginning to be applied to other aspects of ecosystem management

109

(James et al 2013). Certain demographic stages play a disproportionately important role in regulating species population dynamics and identifying these stages is critical to increasing the efficacy of invasive species management (Crandall and Knight 2017). In our study we found that management strategies that focused on limiting overall germination from the soil seedbank were most effective at reducing overall stinknet cover in the system. Although spring-applied herbicides have been shown to provide good short-term control for aboveground cover, our study showed that the spring strategy did not provide effective control into the next year, which is essential to be able to contain the spread of this species. Although we focus on the chemical management of stinknet in this study, we recommend breaking down the life cycle for every focal invasive non-native species (Fig 6). Identifying prominent phenological stages throughout the seasons can help identify mechanisms of invasion, as well as help facilitate the identification of optimal timing for when to manage invasive species populations mechanically, manually, or chemically. For instance, Taylor et al. 2020 found that incorporating information on invasive species phenological life cycles into invasive plant control management plans dramatically improved efforts to eradicate focal invasive species within degraded lands that are undergoing restoration. Our results further highlight the importance of aligning management treatments with the right demographic stage of the focal invader to maximize the efficacy of invasive plant control.

The success of invasive plant management for rapidly spreading short-lived invaders is often contingent on reducing fecundity (Ramula et al 2008). When working with species such as stinknet that are highly fecund, and that produce relatively small

seeds that are easily dispersed (Fig. 6D), strategies that target the seedbank where these

fecundity impacts can accumulate are often key in reducing the invader cover

(Norsworthy et al. 2018; Gioria et al. 2014). Our research found that applying herbicides

during the fall season not only hindered the establishment of our targeted invasive species

but also led to a reduction in seed production, providing better invader control. Although

we did not observe control of stinknet cover one year after treatment under the spring

strategy, spring-applied post-emergent herbicides have been observed to be effective at

killing invasive species one month after treatment, within the same growing season

(McDonald & Rodriguez, unpublished data). Therefore, applying herbicides within the

spring season may still be a viable strategy to control stinknet cover, but only during

earlier stages of invasion when the invader seedbank is not yet abundant (Fig. 6B).

Moreover, the phenological stage of the plant at the time of treatment within the spring

can mediate whether invasive species are able to still produce viable seed. In our study,

we applied spring herbicide treatments when 5% of the population entered the

budding/flowering stage in late March/early April (Fig. 6C), however this stage may have

allowed for viable seeds to be produced and added to the seedbank (Mirsky et al. 2009;

Ziska, 2016). Applying post-emergent herbicides before plants begin to bud can reduce

stinknet seed viability by up to 99% (Douglas & Nicholson, 2019). Moreover, in areas

with variable climates where environmental conditions can cause phenological shifts in

the timing and amount of fruit production (Piao et al. 2019; Gordo & Sanz, 2012),

managing invaders may require flexible field schedules to change timing of herbicide

applications to align with the appropriate phenological stage to maximize efficacy of

invader control. These findings suggest that in areas where temporal variability may be high, applying herbicides when flowering has already begun may not be an optimal strategy for controlling stinknet. Further research is required to assess the viability and density of seeds produced from individuals treated directly with herbicides during different phenological stages of the growing season.

Repeated invader control actions such as multiple years of herbicide application are often a key component of invasive plant management (Rohal et al. 2021). However, we did not observe a clear outcome from our multiple years of herbicide application. The increased density of seeds may be an artifact of the timing of seedbank collection, which included an extra year of un-treated growing season propagules, residual plant cover on the plots, and/or the high reproductive output of stinknet. The relationship between two herbicide applications and increasing stinknet seed density in our study was primarily driven by the positioning of our experimental blocks at one of our study sites. At the Motte Rimrock Reserve, our second-year application was positioned downslope of the one-year treatment block. Given that the seeds are dispersed by wind and water, rain events could have facilitated the movement of seeds downslope, increasing seed density in downslope blocks (Larios et al. 2013; Scherricks et al. 2022). When we removed the downslope experimental block at Motte from the analysis, the two years of herbicide application effect disappeared. Future studies should always account for landscape position when designing effective invasive plant management plans. Additionally, repeated herbicide use may not be the best way to maintain native diversity, as we observed a decrease in the gap between aboveground and seedbank diversity after two

112

years of treatment (Fig. 6E). These results highlight the challenges when managing

species that are capable of inputting large amounts of seeds into the seedbank annually or

are dispersing from nearby source populations.

Our findings also suggest that the length of time the herbicides remained active in

the soil may be an important factor in managing invader populations in the long term. For

instance, fall herbicides used in the fall-applied strategy had soil residual activities that

could last up to 18 months after treatment (Shaner, 2014), which would explain why we

observed that invader cover was consistently low across all the fall-applied strategies

regardless of the number of applications. Further, because of this residual soil activity, it

is possible that our one year after sampling did not completely capture the longer-term

effects of multiple applications. Future studies should try to incorporate sampling

multiple years after treatments have been applied to gain a better understanding of

species recovery in treated plots. Similarly, spring-applied clopyralid, which can also

remain active in the soil for up to 18 months after application (Shaner, 2014),

significantly reduced stinknet cover one year after treatment compared to the other

spring-applied herbicides. In contrast to clopyralid, glyphosate and triclopyr applied in

the spring, both of which have short windows of soil activity, contained similar stinknet

cover to control plots one year after application. Differences in seed dormancy and

longevity can also greatly impact invader persistence over time (Fumanal et al. 2008),

and these traits advocate for designing a multi-year management plan that accounts for

the natural history strategies of the focal invader. Although, if you plan on applying

herbicides repeatedly over several years, it is highly advisable to use tank mixes that

contain multiple modes of action to help minimize the risk of developing herbicide resistance issues (Heap & Duke, 2018; Beckie, 2011; Hutchinson et al. 2007).

Recovery potential is contingent on secondary impacts of management strategies and invader legacies

Recovery potential of a site is highly contingent on secondary impacts of invasive plant management strategies on secondary invaders, native species, and overall invader legacies. In our study, we found that the structure of aboveground composition (e.g., litter, bare, native cover, etc.) did not vary between spring-applied and control plots. However, we observed that fall-applied herbicides were associated with significantly higher percent litter and bare ground cover one year after treatment compared to both spring-applied and control plots. Increased litter from non-native annual grasses, which are some of the main invaders of California grasslands, may limit the establishment of native species via microsite modifications such as increased shading and nutrient deposition (Wainwright et al. 2017; Dudney et al. 2016). Accumulation of litter has been found to decrease the germination and growth rates of native forbs in California grasslands (LaForgia, 2021; Schwab et al. 2023). These dynamics may promote secondary invasion from resource-acquisitive invasive species that reside in the areas surrounding post-treated areas (D'Antonio & Meyerson, 2002; Pearson et al. 2018). Although bare ground patches can promote re-establishment and secondary invasion, this blank slate also provides opportunities for intervention and assisted recovery. For instance, the overall low establishment of both native and non-native species in fall-applied plots suggest that active restoration through trait-based seed mixes or

114

revegetation efforts are likely needed to assist the recovery of native plant communities (Funk et al. 2008; Schuster et al. 2018).

Despite these changes in aboveground composition, the seedbank density of native species in the soil was not depleted by any of the management treatments. Unlike many invasive species that have transient seedbanks, California native species often have long-lived seedbanking strategies that may act as a buffer to mediate short term management impacts (Larson & Suding, 2022; Gremer & Sala, 2013). However, the native seedbank may still be insufficient to promote native recovery, especially in sites that have been more degraded or have had a long history of invasion (Larios & Suding, 2013). Notably, while the native seedbank may not be depleted, its composition may shift with invasion which may prevent restoration (Cox and Allen 2008). While our field site is now dominated by annual species, it was likely a Riversidean sage scrub community dominated by shrubs. In our seedbank sampling effort, shrub species were not present. These results suggest that herbicide treatments alone are not enough to prompt native plant recovery and should be followed by active restoration such as sowing seeds and/or transplanting natives to suppress reinvasion and promote native plant recovery (Bucharova & Krahulec, 2020; Schuster et al. 2017).

In closing, the continuous spread of invasive species and reduction in native biodiversity highlights the need for effective integrated plant management to help restore degraded landscapes. In this study we found that in response to a variety of herbicide treatments, above ground cover and below ground seedbank responses were not always consistent. In this era of unprecedented climate change, the way we evaluate options for

invasive plant management and restoration of native species require assessments under a variety of environmental conditions to be able to predict species responses (Engel et al. 2011; Giejsztowt et al. 2019; Schlaepfer & Lawler, 2023). We encourage studies to investigate aboveground and seedbank responses of both the focal invader and native species to management treatments under variable conditions, whilst keeping the phenological life cycle of the focal invader in mind to identify suitable strategies for invasive plant management that encompass broader restoration goals.

References.

A.H. SA, Shahen M, Ali EF, Majrashi A, M, Eid S.D., Khaffagy AE, Ageba MF (2022) Improving integrated management of weed control by determination of weed seedbank in sandy and clay soil. Saudi Journal of Biological Sciences, 29:3023-3032

Anderson, M.J. (2001), A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26: 32-46

Bahm, M., Barnes, T., & Jensen, K. (2011). Herbicide and Fire Effects on Smooth Brome (Bromus inermis) and Kentucky Bluegrass (Poa pratensis) in Invaded Prairie Remnants. Invasive Plant Science and Management, 4(2), 189-197

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1–48

Beckie, H. (2014). Herbicide Resistance in Weeds and Crops: Challenges and Opportunities. In: Chauhan, B., Mahajan, G. Recent Advances in Weed Management. Springer, New York, NY

Brudvig, L.A., Barak, R.S., Bauer, J.T., Caughlin, T.T., Laughlin, D.C., Larios, L., Matthews, J.W., Stuble, K.L., Turley, N.E. and Zirbel, C.R. (2017), Interpreting variation to advance predictive restoration science. Journal of Applied Ecology, 54: 1018-1027

Bucharova A, Krahulec F (2020) Native seed addition as an effective tool for post-invasion restoration. Basic and Applied Ecology 42:54–6

Cleland EE, Collins SL, Dickson TL, Farrer EC, Gross KL, Gherardi LA, Hallett LM, Hobbs RJ, Hsu JS, Turnbull L, Suding KN (2013), Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. Ecology 94:1687–1696

Copeland, S.M., Munson, S.M., Bradford, J.B., Butterfield, B.J. and Gunnell, K.L. (2019), Long-term plant community trajectories suggest divergent responses of native and non-native perennials and annuals to vegetation removal and seeding treatments. Restoration Ecology, 27: 821-831

Corbin, J.D., and D'Antonio, C. (2012) Gone but Not Forgotten? Invasive Plants' Legacies on Community and Ecosystem Properties. Invasive Plant Science and Management, vol. 5, no. 1, pp. 117–124

Cox, R.D., Allen, E.B. (2008), Composition of soil seedbanks in southern California coastal sage scrub and adjacent exotic grassland. Plant Ecology 198, 37–46

Crandall RM, Knight TM (2018) Role of multiple invasion mechanisms and their interaction in regulating the population dynamics of an exotic tree. The Journal of Applied Ecology 55:885–894

D'Antonio, C. and Meyerson, L.A. (2002), Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. Restoration Ecology, 10: 703-713

Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592:571–576

Dickens, S.J.M., Mangla, S., Preston, K.L. and Suding, K.N. (2016), Embracing variability: environmental dependence and plant community context in ecological restoration. Restoration Ecology, 24: 119-127

Douglas, A. and D. Nicholson. 2019. Biology and Management of matricaria (Oncosiphon piluliferum)

Dudney, J., Hallett, L.M., Larios, L., Farrer, E.C., Spotswood, E.N., Stein, C. and Suding, K.N. (2017), Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands?. Journal of Ecology, 105: 484-495

Engel K, Tollrian R, Jeschke JM (2011) Integrating biological invasions, climate change and phenotypic plasticity. Communicative & Integrative Biology 4:247–250

Flory, S.L. and Clay, K. (2009), Invasive plant removal method determines native plant community responses. Journal of Applied Ecology, 46: 434-442

Fumanal B, Gaudot I, Bretagnolle F (2008) Seed-bank dynamics in the invasive plant, Ambrosia artemisiifolia L. Seed Science Research 18:101–114

Gaskin JF, Espeland E, Johnson CD, Larson DL, Mangold JM, McGee RA, Milner C, Paudel S, Pearson DE, Perkins LB, Prosser CW, Runyon JB, Sing SE, Sylvain ZA, Symstad AJ, Tekiela DR (2021) Managing invasive plants on Great Plains grasslands: A discussion of current challenges. Rangeland Ecology & Management 78:235–249. Giejsztowt J, Classen AT, Deslippe JR (2020) Climate change and invasion may synergistically affect native plant reproduction. Ecology 101:e02913

Gioria, M., Carta, A., Baskin, C.C., Dawson, W., Essl, F., Kreft, H., Pergl, J., van Kleunen, M., Weigelt, P., Winter, M. and Pyšek, P. (2021), Persistent soil seedbanks promote naturalization and invasiveness in flowering plants. Ecology Letters, 24: 1655-1667

Gioria M, Jarošík V, Pyšek P (2014) Impact of invasions by alien plants on soil seedbank communities: Emerging patterns, Perspectives in Plant Ecology, Evolution and Systematics, 16:132-142

Gioria M, Osborne BA (2014) Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5:501

Gioria M, Pyšek P (2015) The Legacy of Plant Invasions: Changes in the Soil Seedbank of Invaded Plant Communities. Bioscience 66:40–53

Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. Global Change Biology 16:1082–1106

Gremer JR, Sala A (2013) It is risky out there: the costs of emergence and the benefits of prolonged dormancy. Oecologia 172:937-947

Harrison S, Spasojevic MJ, Li D (2020) Climate and plant community diversity in space and time. Proceedings of the National Academy of Sciences of the United States of America 117:4464–4470

Heap I, Duke SO (2018) Overview of glyphosate-resistant weeds worldwide. Pest management science 74:1040–1049

Hedrick, P.W, McDonald, C.J. (2020) Stinknet, A New Invasive, Non-native Plant in the Southwestern United States. Desert Plants. 36:5–16

Hobbs RJ, Mooney HA (1995) Spatial and Temporal Variability in California Annual Grassland: Results from a Long-Term Study. Journal of Vegetation Science, 6:43–56

James JJ, Sheley RL, Erickson T, Rollins KS, Taylor MH, Dixon KW (2013) A systems approach to restoring degraded drylands. Journal of Applied Ecology 50:730–739

Jepson Flora Project (2023) Jepson eFlora. https://ucjeps.berkeley.edu/eflora/

Jurand BS, Abella SR, Suazo AA (2013) Soil seedbank longevity of the exotic annual grass Bromus rubens in the Mojave Desert, USA. Journal of Arid Environments 94:68–75

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48:970–979

Kiss, R., Deák, B., Török, P., Tóthmérész, B. and Valkó, O. (2018), Grassland seedbank and community resilience in a changing climate. Restoration Ecology, 26: S141-S150

Kyser GB, Peterson V, Orloff SB, Wright SD, DiTomaso JM (2011) Control of Yellow Starthistle (Centaurea solstitialis) and Coast Fiddleneck (Amsinckia menziesii) with Aminopyralid. Invasive Plant Science and Management 4:341–348

LaForgia ML (2021) Impacts of invasive annual grasses and their litter vary by native functional strategy. Biological Invasions 23:2621–2633

LaForgia ML, Spasojevic MJ, Case EJ, Latimer AM, Harrison SP (2018) Seedbanks of native forbs, but not exotic grasses, increase during extreme drought. Ecology 99:896–903

Larios, L., Aicher, R.J. and Suding, K.N. (2013), Effect of propagule pressure on recovery of a California grassland after an extreme disturbance. Journal of Vegetation Science, 24: 1043-1052

Larios, L., Suding, K.N. (2013). Restoration Within Protected Areas: When and How to Intervene to Manage Plant Invasions?. In: Foxcroft, L., Pyšek, P., Richardson, D., Genovesi, P. Plant Invasions in Protected Areas. Invading Nature–- Springer Series in Invasion Ecology, vol 7:599-618

Larson JE, Suding KN (2022) Seedbank bias: Differential tracking of functional traits in the seedbank and vegetation across a gradient. Ecology 103:e3651

Lazarus BE, Germino MJ (2022) Plant community context controls short- versus medium-term effects of pre-emergent herbicides on target and non-target species after fire. Applied Vegetation Science 25:e12662

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

Michael P, Yeoh P, Ota N, Scott J (2011) Climate Change Impacts on Agricultural Weeds in Western Australia. https://espace.curtin.edu.au

Mirsky SB, Curran WS, Mortensen DA, Ryan MR, Shumway DL (2009) Control of cereal rye with a roller/crimper as influenced by cover crop phenology. Agronomy journal 101:1589–1596

Norsworthy JK, Korres NE, Bagavathiannan MV (2018) Weed Seedbank Management: Revisiting How Herbicides Are Evaluated. Weed Science 66:415–417

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, ''Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Braak C, Weedon J (2022). _vegan: Community Ecology Package_. R package version 2.6-2, <https://CRAN.R-project.org/package=vegan>

Pearson DE, Ortega YK, Runyon JB, Butler JL (2016) Secondary invasion: The bane of weed management. Biological Conservation 197:8–17

Piao S, Liu Q, Chen A, Janssens IA, Fu Y, Dai J, Liu L, Lian X, Shen M, Zhu X (2019) Plant phenology and global climate change: Current progresses and challenges. Global Change Biology 25:1922–1940

Prior KM, Adams DC, Klepzig KD, Hulcr J (2018) When does invasive species removal lead to ecological recovery? Implications for management success. Biological invasions 20:267–283

Rohal CB, Cranney C, Hazelton ELG, Kettenring KM (2019) Invasive Phragmites australis management outcomes and native plant recovery are context dependent. Ecology and Evolution 9:13835–13849

Rohal CB, Reinhardt Adams C, Reynolds LK, Hazelton ELG, Kettenring KM (2021) Do common assumptions about the wetland seedbank following invasive plant removal hold true? Divergent outcomes following multi-year Phragmites australis management. Applied Vegetation Science 24:e12626

Roiloa SR, Yu F-H, Barreiro R (2020) EDITORIAL: Plant invasions: Mechanisms, impacts and management. Flora 267:151603

Silva GHM, Overbeck GE (2020) Soil seedbank in a subtropical grassland under different grazing intensities. Acta botanica Brasilica. 34(2): 360-370

Schlaepfer MA, Lawler JJ (2023) Conserving biodiversity in the face of rapid climate change requires a shift in priorities. Wiley interdisciplinary reviews. Climate change 14

Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. Journal of Applied Ecology 55:2362–2373

Schwab ST, Jenerette GD, Larios L (2023) Prescribed burning may produce refugia for invasive forb, Oncosiphon pilulifer. Restoration Ecology 31:e13922

Schwartz-Lazaro LM, Copes JT (2019) A Review of the Soil Seedbank from a Weed Scientists Perspective. Agronomy 9:369

Shaner, D.L. (2014) Herbicide Handbook. 10th Edition, Weed Science Society of America

Skurski TC, Maxwell BD, Rew LJ (2013) Ecological tradeoffs in non-native plant management.Biological Conservation 159:292–302

Wainwright, C.E., Dwyer, J.M. & Mayfield, M.M. (2017) Effects of exotic annual grass litter and local environmental gradients on annual plant community structure. Biological Invasions 19:479–491

Weidlich EWA, Flórido FG, Sorrini TB, Brancalion PHS (2020) Controlling invasive plant species in ecological restoration: A global review. Journal of Applied Ecology 57:1806–1817

Ziska LH (2016) The role of climate change and increasing atmospheric carbon dioxide on weed management: Herbicide efficacy. Agriculture, Ecosystems & Environment 231:304–309

Figures & Apendices.
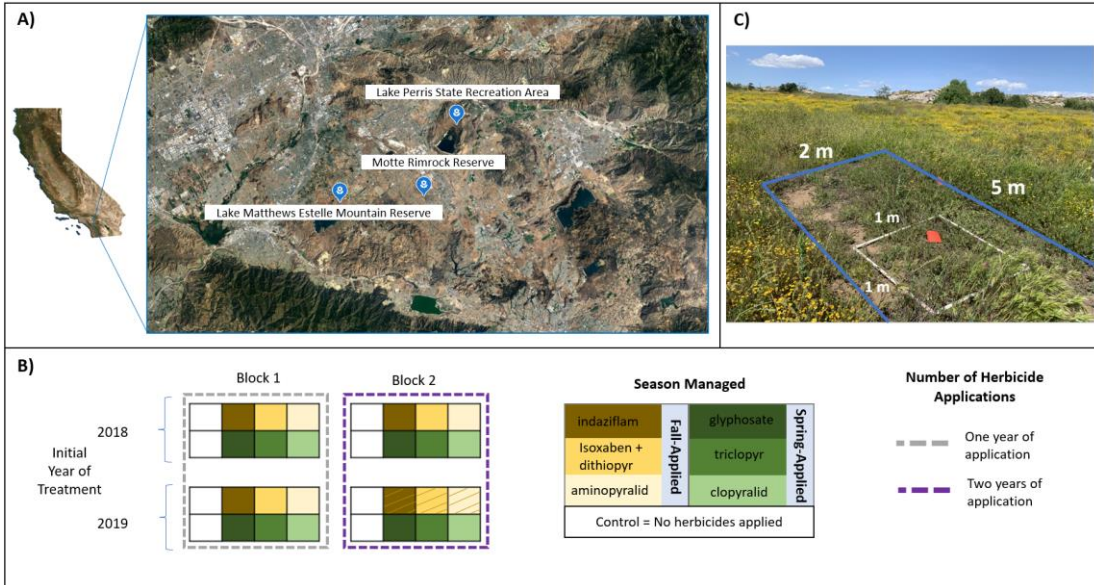
Figure 1. A) Study sites: Lake Matthew Estelle Mountain Reserve, Lake Perris State Recreation Area, Motte Rimrock Reserve in California, USA. B) Study design layout for herbicide application implemented at each site. Colors represent individual herbicide treatments. Gray dashed lines indicate blocks that were treated once with herbicide, while purple dashed lines indicated two applications of herbicides. Plots are shown grouped together for clarity but were randomly assigned to treatments within a block and were spaced apart. Horizontal filling of plots indicate plots that did not receive two years of treatment due to COVID-19 restrictions. C) Composition data was taken within a 1 x 1m subplot within the larger 2 x 5 m experimental plot. Note the yellow stinknet inflorescences across the landscape.
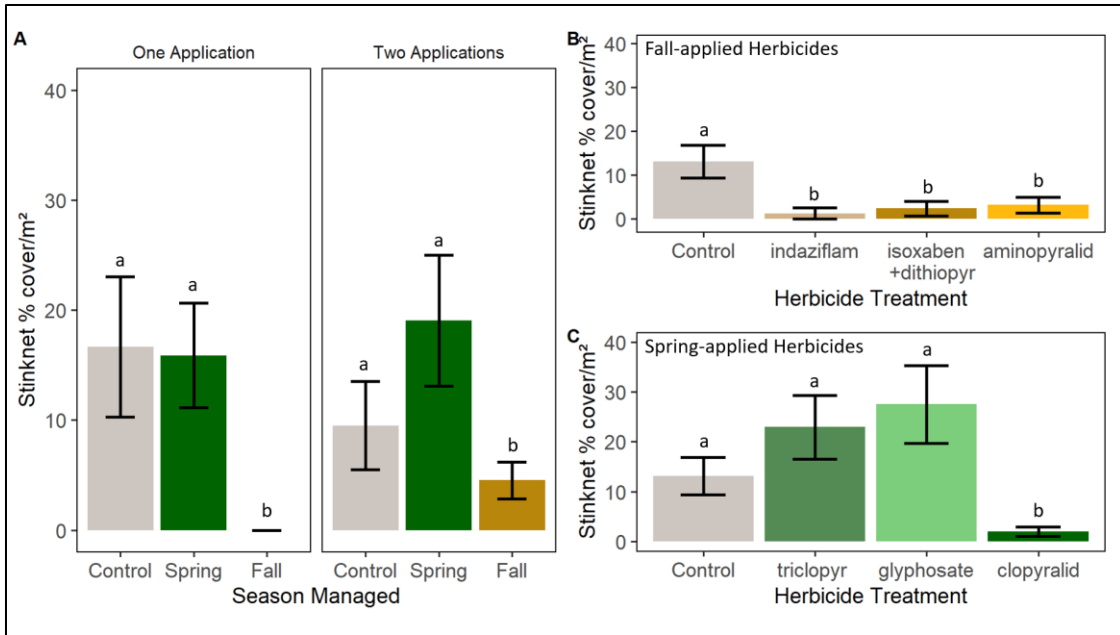
Figure 2. Average aboveground stinknet cover by A) season managed x number of applications, B) Fall-applied herbicide treatments, and C) Spring-applied herbicide treatments. Colors represent season managed. Letters represent significant differences. Bars are mean + 1 SE.
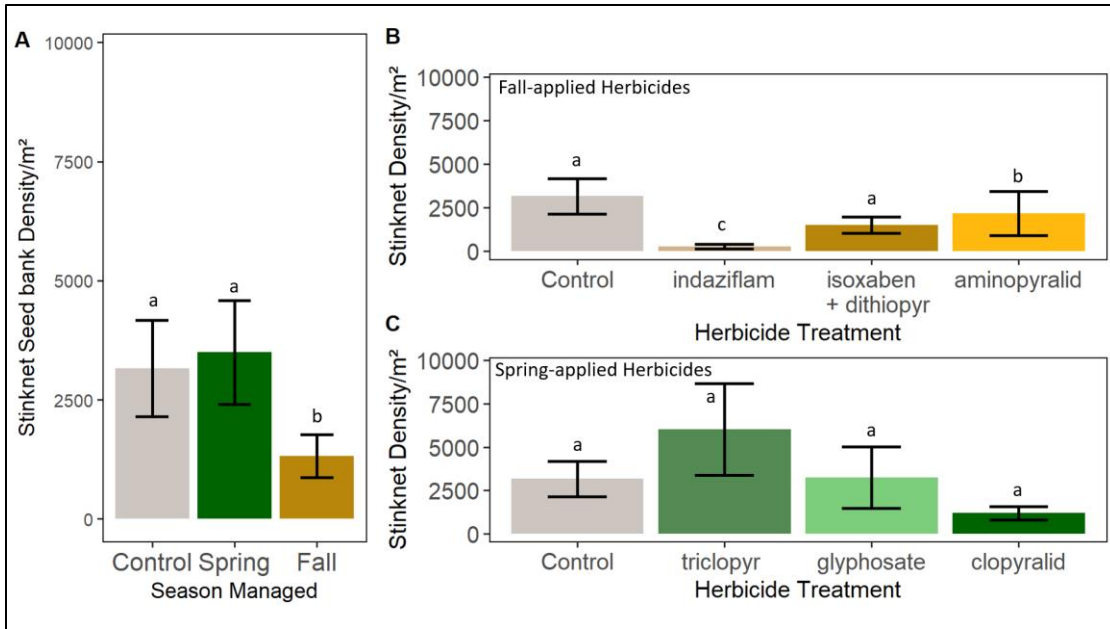
Figure 3. Belowground stinknet seedbank density per meter squared A) by season managed, B) by Fall-applied herbicide treatments, C) by Spring-applied herbicide treatments. Colors represent season managed Letters represent significant differences. Bars are mean + 1 SE.
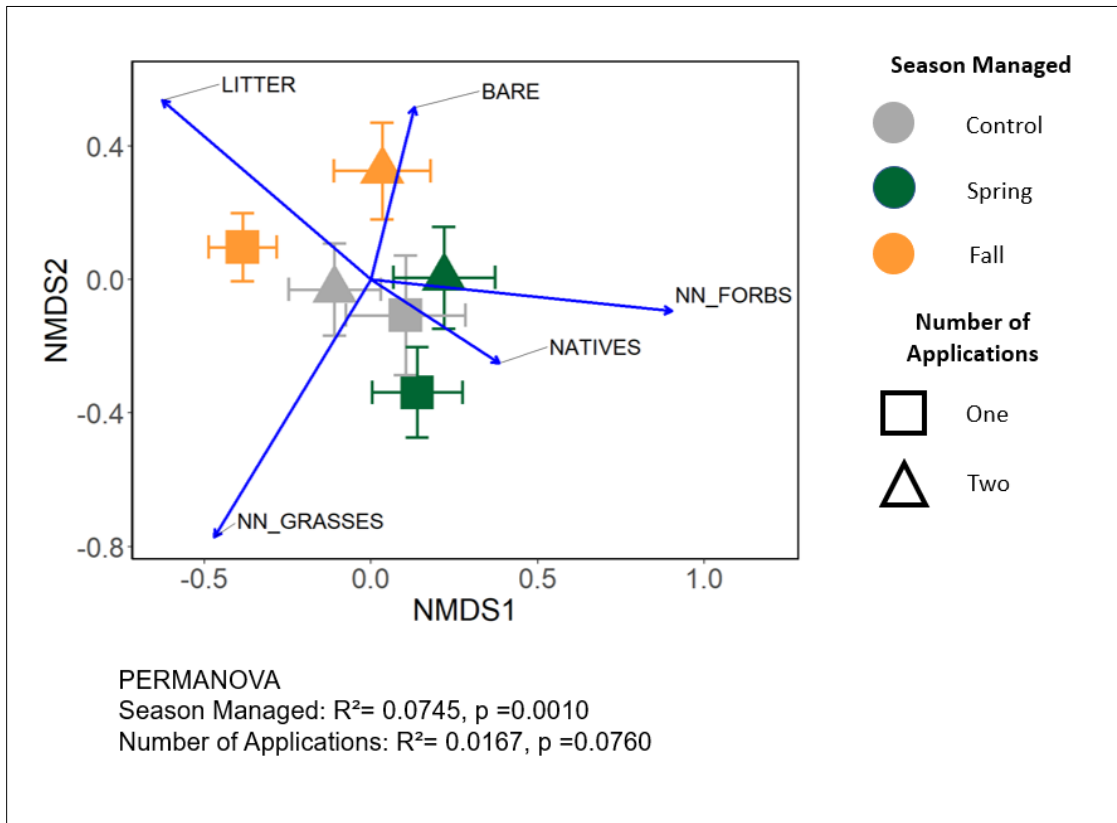
Figure 4. Non-metric multidimensional scaling (NMDS) plot of aboveground plant community composition based on Bray Curtis dissimilarity. Species were grouped into natives, non-native forbs, and non-native grasses. Color represents season managed, while shapes (■) represent plots that received one application of herbicide, and (▲) represent plots that received two applications of herbicide. Error bars are 1SE.
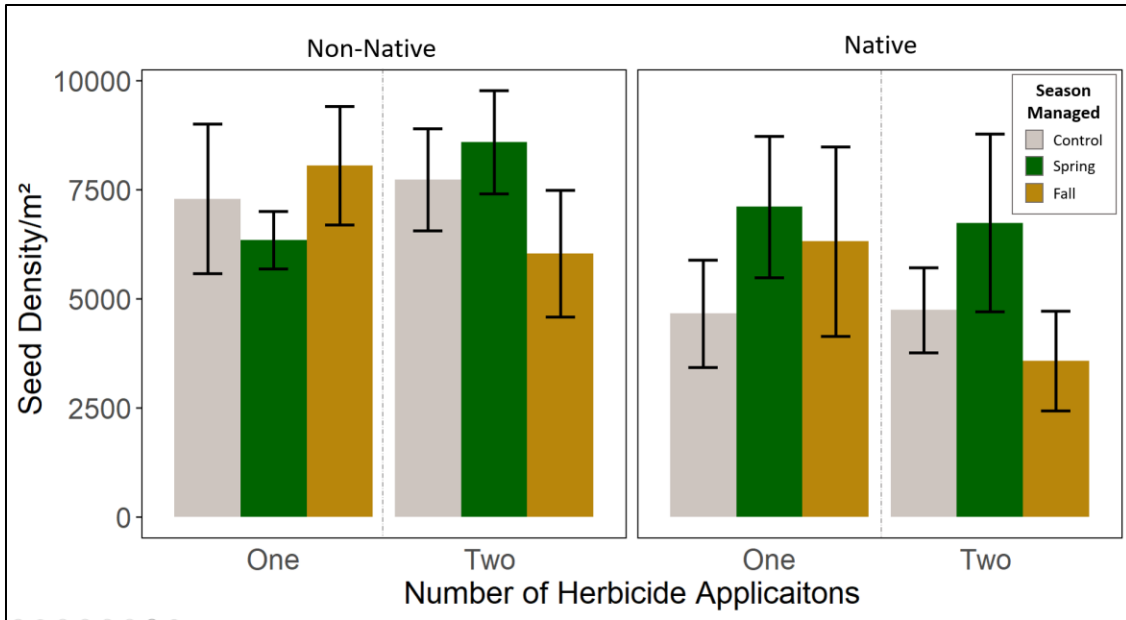
Figure 5. Seed density of non-target species per meter squared by season managed, number of applications and species origin: non-native (not including stinknet) and native. Colors represent season managed. Error bars are 1 SE.
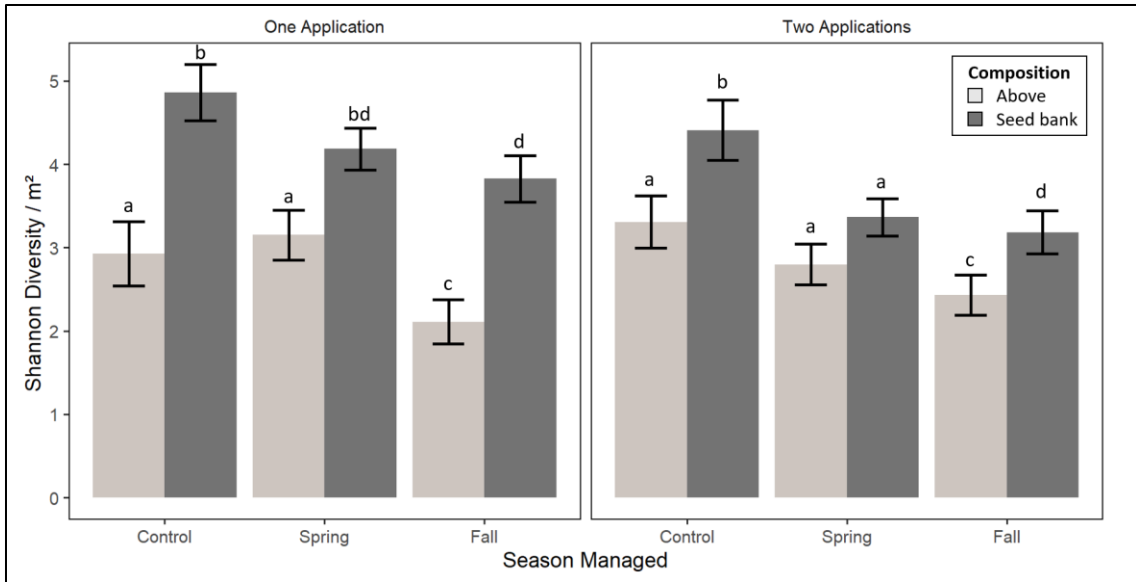
Figure 5. Shannon Diversity of aboveground composition (light grey) and seedbank composition (dark grey) by herbicide strategy and number of herbicide applications. Letters denote statistical differences.
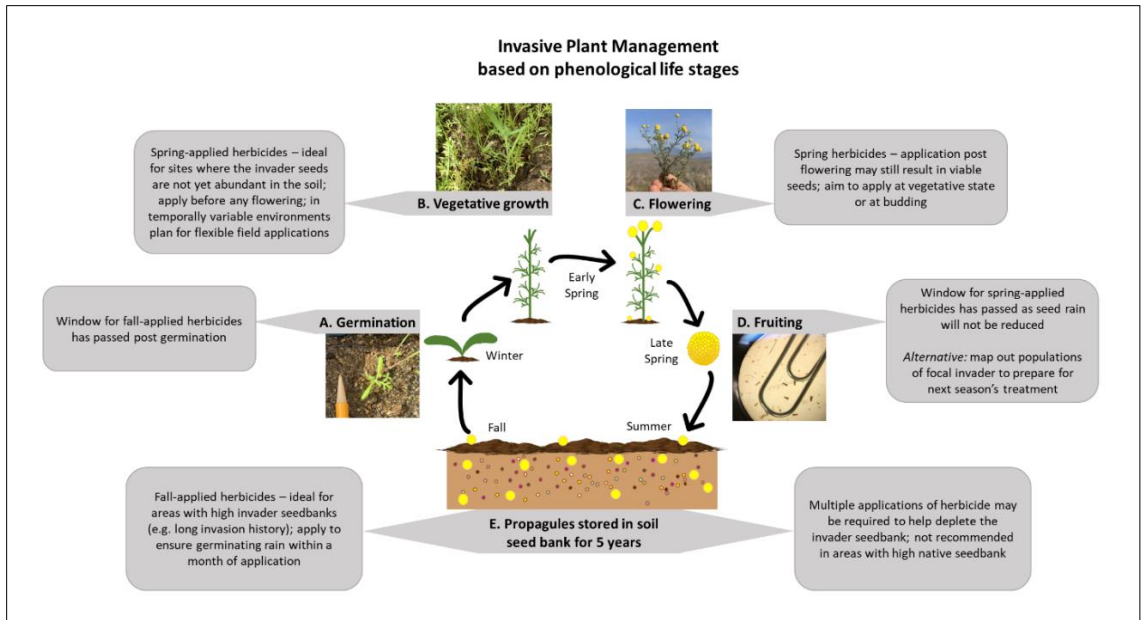
Figure 6. Life cycle of stinknet separated into 5 phenological stages that can be used to inform how to best manage this focal invader. A) Germination begins in the winter, note the pencil for scale. B) Period of vegetative growth from winter-early spring. C) Flowering mid to late spring. D) Fruiting late spring to early summer, each inflorescence contains up to 300 miniscule seeds, note the paperclip for scale. E) Seeds are deposited in the soil and remain viable for 5 years.

Supplementary Information.
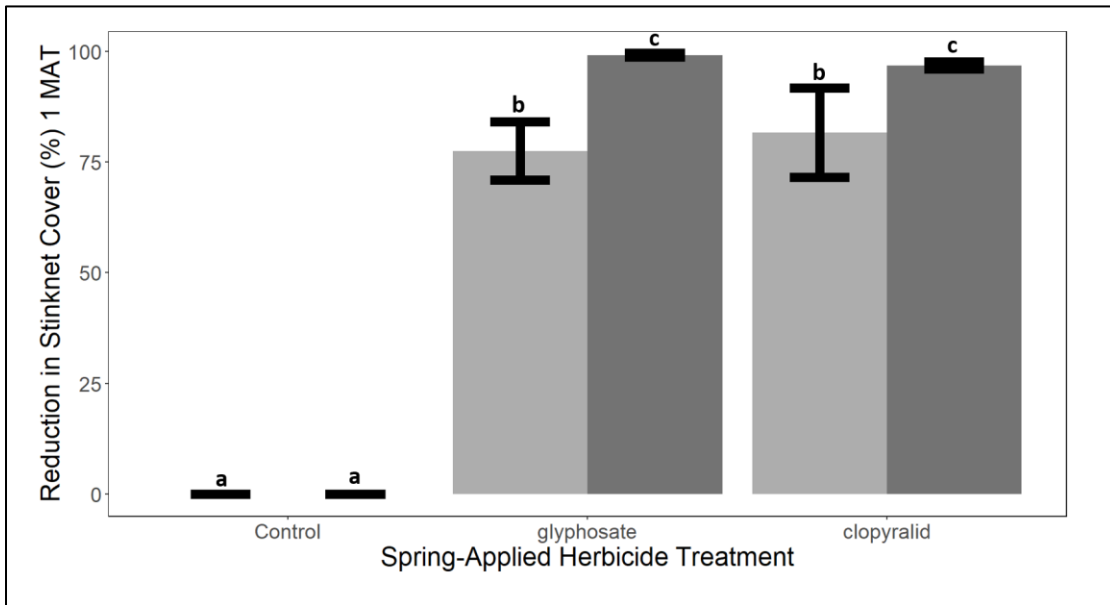
Figure S1. Reduction in Stinknet Cover (%) one month after treatment by Herbicide treatment. Light gray represents plots sprayed in 2016, while dark gray represents plots sprayed in 2017. Letters represent significant differences. Data are reported as means ±1 SE

Table S1. Average growing season temperature and precipitation derived from PRISM Climate Group for 2017-2021.

Site Oct-Jun	Lake Matthews	Lake Perris	Motte Rimrock	AVG across three sites	Growing Season
Precipitation (mm)	288	294	354	312	**2016-2017**
Mean Temp (° C)	16.92	16.92	16.56	16.81	
Precipitation (mm)	100	99	106	102	**2017-2018**
Mean Temp (° C)	17.39	16.84	17.12	17.11	
Precipitation (mm)	337	337	406	373	**2018-2019**
Mean Temp (° C)	15.53	14.93	14.98	15.15	
Precipitation (mm)	341	316	362	340	**2019-2020**
Mean Temp (° C)	16.25	15.32	15.24	15.6	
Precipitation (mm)	116	125	137	126	**2020-2021**
Mean Temp (° C)	16.42	15.96	16.15	16.17	

Table S2. List of herbicides and concentrations used in experimental trials. No adjuvants were used with the herbicides.

* "a.e." = acid equivalent; ** "a.i." = active ingredient

Herbicide Strategy	Herbicide Name	Active Ingredient	Concentration	Herbicide applied per plot
Pre-Emergent	Milestone	aminopyralid	7 oz/ac (2 lb/g a.e. formulation)*	0.52 ml/plot
Pre-Emergent	Esplanade	indaziflam	7 oz/ac (1.67 lb/g a.i. formulation)**	0.52 ml/plot
Pre-Emergent	Gallery + Dimension	Isoxaben + dithiopyr	16-31 oz/ac (4.16 lb/g a.i. formulation)/ 2 qt/ac (1 lb/g a.i. formulation)	2.3 ml Garlon + 2.4 ml Dimension/plot
Post-Emergent	Roundup	glyphosate	4 qt/ac (4 lb/g a.e. formulation)	9.5 ml/plot
Post-Emergent	Transline	clopyralid	⅔ pt/ac (3 lb/g a.e. formulation)	0.80ml/plot
Post-Emergent	Garlon	triclopyr amine or ester (ester preferred, but depends on wetland status)	8 qt/ac (3 lb/g a.e. formulation) or 1-4 qt/ac (4 lb/g a.e. formulation)	19ml/plot

Table S3. Dates of herbicide applications over the course of the study. Applications in Fall were applied in November, just before germinating rains while applications in the Spring were dependent on the phenology of stinknet, when stinknet was starting to bud and <5% of the population was flowering.

Year Treated	Fall Application Date	Spring Application Date
2018	November 8, 2018	April 9, 2018
2019	November 15, 2019	Mar 19, 2019
2020	* Application canceled due to COVID-19	Mar 6th, 2020

Table S4. Species list and six letter species codes observed in the study.

CODE	Scientific Name	Origin
ACMSTR	*Acmispon strigosus*	native
AMAALB	*Amaranthus albus*	nonnative
AMSMEN	*Amsinckia menziesii*	native
ARIPUR	*Aristida purpurea*	native
ATRSEM	*Atriplex semibaccata*	nonnative
AVEBAR	*Avena barbatus*	nonnative
AVEFAT	*Avena fatua*	nonnative
BACPIL	*Baccharis pilularis*	native
BRANIG	*Brassica nigra*	nonnative
BRODIA	*Bromus diandrus*	nonnative
BROMAD	*Bromus madritensis*	nonnative
CALMEN	*Calandrinia menziesii*	native
CAMBIS	*Camissoniopsis bistorta*	native
CAULAS	*Caulanthus lasiophyllus var. rigidus*	native
CRACON	*Crassula connata*	native
CROSET	*Croton setiger*	native
CRYINT	*Cryptantha intermedia*	native
DEIFAS	*Deinandra fasciculata*	native
DEIKEL	*Deinandra kelloggii*	native
DICCAP	*Dichelostemma capitatum*	native
EROBOT	*Erodium botrys*	nonnative
EROCIC	*Erodium cicutarium*	nonnative
EROMUS	*Erodium moschatum*	nonnative

EUPALB	*Euphorphia albomarginata*	native
EURGUT	*Erythranthe guttata*	native
GILANG	*Gilia angelensis*	native
HIRINC	*Hirschfeldia incana*	nonnative
HORMUR	*Hordeum murinum*	nonnative
HYPGLA	*Hypochaeris glabra*	nonnative
LACSER	*Lactuca serriola*	nonnative
LASCAL	*Lasthenia californica*	native
LAYPLA	*Layia platyglossa*	native
LEPNIT	*Lepidium nitidum*	native
LUPBIC	*Lupinus bicolor*	native
MALPAR	*Malva parvifolia*	nonnative
OENSP	*Camissoniopsis hirtella*	native
ONCPIL	*Oncosiphon piluliferum*	nonnative
Plagiobot	*Plagiobothrys sp.*	native
SALTRA	*Salsola tragus*	nonnative
SCHBAR	*Schismus barbatus*	nonnative
SISIRI	*Sisymbrium irio*	nonnative
SISOFI	*Sisymbrium officinale*	nonnative
SONOLE	*Sonchus oleraceus*	nonnative
TRIALB	*Trifolium albopurpureum*	native
TRILAN	*Trichostema lanceolatum*	native
UROLIN	*Uropapus lindleyi*	native

Table S5: Summary model statistics for Analysis of variance (ANOVA) of stinknet cover as a function of season managed, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF(Num, Den)	F value	*p* value
Season Managed	2,82	13.4945	**<0.0001**
Year Treated	1,0	6.5274	1.0000
Second Application	1,0	0.1337	1.0000
Season Managed: Year Treated	2,82	2.5113	0.0873
Season Managed: Second Application	2,82	1.8913	0.1574
Year Treated: Second Application	1,0	0.2337	1.0000
Season Managed: Year Treated: Second Application	2,82	0.3716	0.6907

Table S6: Summary model statistics for Analysis of variance (ANOVA) of stinknet cover as a function of Fall applied and spring-applied treatments, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF(Num, Den)	F value	*p* value
Fall-Applied Treatments			
Fall Treatments	3,42	6.8769	**0.0007**
Year Treated	1,42	2.6594	0.1104
Second Application	1,42	2.1012	0.1546
Season Managed: Year Treated	3,42	2.3142	0.0896
Season Managed: Second Application	3,42	2.1287	0.1109
Year Treated: Second Application	1,42	0.0032	0.9553
Season Managed: Year Treated: Second Application	3,42	0.3452	0.7927
Spring-Applied Treatments			
Spring Treatments	3,42	9.7904	**<0.0001**
Year Treated	1,42	3.1663	0.0824
Second Application	1,42	0.0008	0.9776
Season Managed: Year Treated	3,42	1.2328	0.3097
Season Managed: Second Application	3,42	0.5010	0.6836
Year Treated: Second Application	1,42	0.3595	0.5520
Season Managed: Year Treated: Second Application	3,42	0.0866	0.9670

Table S7: Summary model statistics for Analysis of variance (ANOVA) of amount of stinknet cover controlled as a function of within-season spring treatments, year of herbicide treatment and their interactions. Bolded p values indicate significance <0.05

	DF(Num, Den)	F value	*p* value
Treatment	2,28	60.6026	**<0.0001**
Year Treated	1,2	3.2358	0.2138
Treatment: Year Treated	2,28	8.4812	**0.0013**

Table S8: Summary model statistics for Analysis of variance (ANOVA) of stinknet seed density as a function of season managed, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF(Num, Den)	F value	*p* value
Season Managed	2,80	8.6140	**0.0004**
Year Treated	1,80	0.0063	0.9360
Second Application	1,4	0.0524	0.8300
Season Managed: Year Treated	2,80	0.8797	0.4180
Season Managed: Second Application	2,80	0.7673	0.4680
Year Treated: Second Application	1,80	4.0400	**0.0478**
Season Managed: Year Treated: Second Application	2,80	0.1814	0.8344

Table S9: Summary model statistics for Analysis of variance (ANOVA) of stinknet seed density as a function of fall-applied and spring-applied treatments, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF(Num, Den)	F value	*p* value
Fall-Applied Treatments			
Fall Treatments	3,40	11.9504	**<0.0001**
Year Treated	1,40	0.0777	0.7818
Second Application	1,4	0.1240	0.9166
Season Managed: Year Treated	3,40	0.5081	0.6789
Season Managed: Second Application	3,40	0.1613	0.9217
Year Treated: Second Application	1,40	4.7016	**0.0361**
Season Managed: Year Treated: Second Application	3,40	0.2263	0.8775
Spring-Applied Treatments			
Spring Treatments	3,40	1.3868	0.2608
Year Treated	1,40	0.2792	0.6001
Second Application	1,4	0.1660	0.7044
Season Managed: Year Treated	3,40	1.3782	0.2633
Season Managed: Second Application	3,40	0.7652	0.5203
Year Treated: Second Application	1,40	1.9228	0.1732
Season Managed: Year Treated: Second Application	3,40	0.6574	0.5831

Table S10: Summary model statistics for Permutational Analysis of Variance (PERMANOVA) of aboveground plant community composition as a function of season managed, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF	SS	R²	F value	*p* value
Season Managed	2.0000	1.3842	0.1251	7.0545	**0.0010**
Year Treated	1.0000	0.4137	0.0374	4.2100	**0.0170**
Second Application	1.0000	0.1319	0.0119	1.3447	0.2300
Season Managed: Year Treated	2.0000	0.4222	0.0381	2.1517	0.0630
Season Managed: Second Application	2.0000	0.2802	0.0253	1.4280	0.2200
Year Treated: Second Application	1.0000	0.1444	0.0103	1.4715	0.2120
Season Managed: Year Treated: Second Application	2.0000	0.0521	0.0047	0.2656	0.9070
Residual	84.0000	8.2404	0.7445		
Total	95.0000	11.0690	1.0000		

Table, S11: Summary model statistics for Permutational Analysis of Variance
(PERMANOVA) of seed bank community composition as a function of season managed,
year of herbicide treatment, number of herbicide applications and their interactions.
Bolded p values indicate significance <0.05.

	DF	SS	R²	F value	*p* value
Season Managed	2.0000	0.3447	0.0194	0.9162	0.3540
Year Treated	1.0000	0.2504	0.0141	1.3312	0.1300
Second Application	1.0000	0.5478	0.0308	2.9126	**0.0070**
Season Managed: Year Treated	2.0000	0.2566	0.0144	0.6820	0.5440
Season Managed: Second Application	2.0000	0.1253	0.0071	0.3332	0.9270
Year Treated: Second Application	1.0000	0.0655	0.0037	0.3481	0.7990
Season Managed: Year Treated: Second Application	2.0000	0.3736	0.0210	0.9930	0.2520
Residual	84.0000	15.7998	0.8895		
Total	95.0000	17.7637	1.0000		

Table, S12: Summary model statistics for Analysis of variance (ANOVA) of non-native seed and native seed density as a function of season managed, year of herbicide treatment, number of herbicide applications and their interactions. Bolded p values indicate significance <0.05.

	DF(Num, Den)	F value	*p* value
Invasive Seed Density			
Season Managed	2,80	3.1332	**0.0489**
Year Treated	1,80	0.1003	0.7523
Second Application	1,4	0.4710	0.5296
Season Managed: Year Treated	2,80	0.2518	0.7781
Season Managed: Second Application	2,80	3.3279	**0.0409**
Year Treated: Second Application	1,80	5.5224	**0.0249**
Season Managed: Year Treated: Second Application	2,80	0.4453	0.6422
Native Seed Density			
Season Managed	2,80	2.7003	0.0733
Year Treated	1,80	0.2271	0.6339
Second Application	1,4	0.5893	0.4847
Season Managed: Year Treated	2,80	0.5393	0.5857
Season Managed: Second Application	2,80	0.5385	0.1729
Year Treated: Second Application	1,80	1.7941	0.4856
Season Managed: Year Treated: Second Application	2,80	0.0760	0.9268