DISSERTATION

SPECIES DISTRIBUTION MODELS FOR AND POLICY APPROACHES TO INVASIVE PLANT ECOLOGY AND MANAGEMENT

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ABSTRACT

SPECIES DISTRIBUTION MODELS FOR AND POLICY APPROACHES TO INVASIVE PLANT ECOLOGY AND MANAGEMENT

The ability of abundance-based Species Distribution Models (SDMs) to predict where invasive plants can be abundant, and to what degree, is a powerful research and management tool. Often, invasive plant abundance-based SDMs are created using similar inputs and approaches as occurrence SDMs. However, invasive plant ecology literature suggests that the factors found to control invasive plant abundance are more diverse and contextual, and therefore not entirely interchangeable with factors that control invasive plant occurrence. To ensure invasive plant abundance-based SDMs are leveraging the robust body of knowledge, this paper aims to highlight and summarize the ecological factors underpinning invasive plant abundance and reviews how those factors can be represented within abundance-based SDMs. I find that while the inclusion of invasive plant abundance governing factors often improves abundance-based SDM performance, certain governing factors are ubiquitously represented while others are less commonly accounted for in model creation despite their ecological importance. Barriers to incorporating invasive plant abundance governing factors into abundance-based SDMs often include data limitations or methodological uncertainty. Finally, we provide future research directions that would help address certain barriers and improve our ability to integrate abundance governing factors into SDMs.

Invasive plants, when they become dominant components of a plant community, threaten native species and ecosystem processes. Abundance-based SDMs are gaining traction as a geospatial tool to predict where invasive plants can become abundant and have negative impacts. Biotic interactions influence invasive plant abundance locally but are often not included within the abundance-based SDM creation process. At present, it is unknown to what degree local-scale biotic interactions with other plant species determine locations where invasive plant species can become abundant. Using data from large-scale abundance observations of the invasive plant cheatgrass (*Bromus tectorum*) paired with data from plant communities in the western United States, we quantified the degree to which biotic interactions explain where cheatgrass is abundant beyond what would be anticipated from an abundance-based SDM created with abiotic and landscape context predictors alone. To this end, we fit Generalized Linear Models (GLMs) for different categories of cheatgrass abundance and used the predicted suitability SDM outputs alongside biotic variables, representing known competitive and facilitative interactions, to determine if including biotic interactions improved a model's explanatory power. The addition of biotic variables marginally improved GLMs for low (5-25%) and medium (25+-50%) cheatgrass abundance but displayed greater improved performance for high (50+%) cheatgrass abundance. Most notable amongst the specific biotic variables was the cover of perennial graminoid cover, representing known competitors of cheatgrass, which interacted with SDM environmental suitability to strongly reduce the probability of high cheatgrass abundance. These findings suggest that considering biotic interactions alongside SDM predicted suitability may indeed improve our ability to predict abundance locations of invasive plant species, but potentially only in specific contexts such as where that species can already achieve high abundance.

Invasive plants cost the US billions of dollars each year due to ecological and economic impacts as well as management costs. One of the most common pathways of introduction and spread of invasive plants is through ornamental plant sales. While solutions such as regulations

and voluntary self-bans have been implemented in some instances to mitigate this problem, widespread adoption has not occurred. As such, new alternatives should be explored. Opt-in labeling programs are commonly used throughout the agricultural industry to better inform customers about the products they are purchasing. An opt-in labeling program that consists of a partnership between retailers and governments or non-profit organizations could help reduce the spread of invasive plants by influencing customer behavior. This approach would be less costly to retailers than regulations, create new invasive plant prevention opportunities for governments and non-profits, and better inform consumers about specific invasive plant species.

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DEDICATION

To my wife Emily, for the love, support, grace you have given me throughout this journey and more. To my children, Fennec and Sylvia, who inspire me to be a better person and make the world a better place. To my family, who knew I could achieve more than I thought I ever could. To my many mentors and colleagues, who showed me what it meant to be a scientist. And finally, to the beauty, mystery, and majesty of the natural world, which brings me peace and purpose like no other. Thank you all, I dedicate this work to you.

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CHAPTER 1 - INVASIVE PLANT ABUNDANCE AND SPECIES DISTRIBUTION MODELS (SDMS): A REVIEW OF THE ECOLOGY OF INVASIVE PLANT ABUNDANCE AND ITS INTEGRATION INTO SDMS

Introduction

Invasive plants represent a critical ecological issue of our time. The impacts and costs of invasive plants across ecosystems are well documented (Hoffmann and Broadhurst 2016; Fantle-Lepczyk et al. 2022), and there is an ever increasing need to leverage effective, science-based tools to better detect and manage invasive plant populations. Species distribution models (SDMs) represent a vital technical tool that enables managers, policy makers, and researchers to better understand and predict where invasive plants can persist across the landscape (Elith 2017). While SDMs have been historically focused on species occurrence, the emergence of abundance-based SDMs (Waldock et al. 2022) provides managers and researchers a greater level of detail when it comes to predicting where and when invasive plant populations can become abundant, and therefore problematic (Sofaer, Jarnevich, and Pearse 2018). However, it is reasonable to believe that species occurrence is not equivalent to species abundance. While the presence of a species is governed by processes of colonization and extinction, abundance of a species is governed by

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Key Terminology

Invasive species: A species that occurs outside of its native range whose rapid population growth and spread causes ecological or economic harm.

Species Niche: The combination of environmental factors that define where a species can and cannot persist.

Species Occurrence: A binary measurement indicating whether a species is or is not present in an area.

Species Abundance: A measurement indicating how much or how many of a species is or are, respectively, found in an area, which may include plot, community, or greater scales. Abundance is commonly represented using biomass, cover, or density but may be captured by other measurements.

Species Distribution Model (SDM): A model that uses the species-environment relationship to determine how suitable a given area is to support species occurrence or abundance.

Abundance Governing Factor: Abiotic, biotic, and landscape factors that collectively influence the abundance of a species. These factors define an invasive species' abundance niche.

Scale: The extent of a modeled region. Can vary from very fine (e.g., 1 m^2 plot) to very broad (e.g., global extent).

Spatial Resolution: The size of an individual pixel of a model. Within the context of this manuscript, fine resolution refers to less than 100 m^2 pixels, while coarse refers to greater than 100 m^2 pixel.

Temporal Resolution: The time scale that model data represent. Temporal resolution

Figure 1.1 Key terminology relevant for critical concepts important to invasive plant abundance-based SDMs.

factors that influence population growth and carrying capacity. As the ecological dynamics that control colonization and extinction are only a subset of the factors that influence population growth and carrying capacity, it stands to reason that species occurrence may not be predictive of species abundance.

Unsurprisingly, this distinction between species occurrence and abundance is reflected within the SDM literature. For example, SDMs that predict high suitability for species occurrence poorly correlate with species abundance (Dallas and Hastings 2018). Furthermore, greater climatic suitability, often the strongest predictor of species occurrence, does not translate to greater abundance (Csergő et al. 2017). Plant taxa in particular have low correlation between environmental suitability and abundance (Weber et al. 2017). One common explanation offered is that despite high environmental suitability, uncaptured local-scale processes may be more critical for abundance (Bradley 2016; Waldock et al. 2022). In fact, there is a growing understanding within SDM literature that community level factors may play an important role in determining where a species can be abundant (Coudun and Gégout 2007; Boulangeat, Gravel, and Thuiller 2012; Lynn et al. 2019; Lembrechts, Nijs, and Lenoir 2019; Dallas and Santini 2020). This mirrors a long standing understanding from invasion ecology literature, where many local factors such as competition (Levine, Adler, and Yelenik 2004) or resource availability (M. A. Davis, Grime, and Thompson 2000) are recognized as having strong control over the abundance of an invasive plant species, but are less critical for species occurrence. While there is overlap between the factors that influence invasive plant occurrence and abundance, the fact that these two categories are not completely interchangeable suggests a need to better define and clarify what factors control invasive plant abundance and how these factors are or can be integrated into SDMs. To that end this paper aims to 1.) provide a summary of abundance governing factors identified within invasive plant ecology literature, 2.) detail current practices of how these abundance governing factors are incorporated into abundance-based SDMs, and 3.) identify future research directions, best practice recommendations, and/or barriers to including abundance governing factors in abundance-based SDMs.

Invasive Plants Abundance and SDMs

Abundance-based SDMs are an ideal tool to better understand and predict invasive plant abundance. SDMs are used to create continuous map products that detail an invasive plant's distribution across a study area. This is accomplished by leveraging the relationship between a species' presence and the environment in which it resides, conceptually known as a species niche (Hutchinson 1957; Silvertown 2004; Colwell and Rangel 2009). Once the relationship between species presence and environmental characteristics is defined, different algorithms can be used to extrapolate or interpolate the probability of species presence based on how suitable each area is across the study region (Franklin 2010a). The species-environment relationship can be defined via correlative approach (species-environment relationship derived only from species occurrence data), mechanistic approach (species-environment relationship derived from process-based studies), or a combination of the two (Evans et al. 2016). The applications of SDMs are numerous and include identifying survey areas for detecting new populations of a species, prioritizing where management actions should occur or would be most beneficial, or informing regulatory decision making and policies (Sofaer et al. 2019). Abundance-based SDMs can yield even greater utility to these types of activities as they provide more detailed information about a species-environment relationships over their occurrence SDM counterparts.

Two key differences can be identified between occurrences-based and abundance-based SDMs generally. First while species presence data are suitable for occurrence models, abundance-based SDMs require the use of abundance data. This reflects the fact that occurrence models are depicting a species' ability to persist in an area, while abundance models are depicting a species' ability to achieve certain levels of abundance (Figure 1.2). Studies within the SDM literature have acknowledged that occurrence SDMs are poorly suited to predict species abundance, even when designed specifically to do so (Jiménez-Valverde, Aragón, and Lobo 2021). This intuitively makes sense as abundance data are inherently different from species presence data. The sampling bias for species occurrences and abundance can differ from one another (Beaury et al. 2023) and the process of ensuring data quality has additional considerations given its non-binary nature (Bradley et al. 2018). The second difference, and the focus of this review, is what predictors are selected to use as model inputs that represent the ecological control on species occurrence or species abundance, or both.

Including factors that are specific to or have greater importance to species abundance is critical to creating ecologically realistic abundance-based SDMs (Waldock et al. 2022). Despite the need for these abundance governing factors to be represented in abundance-based SDMs, they are often left out of model creation. One systematic review of plant occurrence SDMs in general found that while covariates relating to temperature and moisture were common in nearly 90% of studies, covariates relating to soils (i.e. resources availability) were present in only 40% of studies, and covariates relating to biotic interactions or disturbance were present in only 20% of studies (Mod et al. 2016). While this review is specific to occurrence SDMs, it highlights how common it is for SDMs to be created with a limited subset of ecological controls relevant to a species' distribution. Additionally, of the predictor categories analyzed in this study, many of the types of predictors absent from SDM creation are those attributed to having greater influence over invasive plant abundance. Abundance-based SDMs that lack appropriate model predictors may fail to capture essential dynamics pertaining to invasive plant abundance, thus producing models that perform well but are not reflective of ecological reality.

While the impetus to include abundance governing factors across all taxa exists, representing these factors within abundance-based invasive plant SDMs is paramount. Invasive plant abundance, which is defined as a relevant measurement (such as cover, density, and/or biomass (Parker et al. 1999) of how much or many of an invasive plant is or are, respectively, within a given area or community, is a critical component in quantifying invasive plant impacts (Sofaer, Jarnevich, and Pearse 2018; Bradley et al. 2019). As such, abundance is a common measurement of interest for researchers and managers, resulting in a large body of evidence regarding how and when invasive plants become abundant. Given our increasing ability to model invasive plant abundance, it is paramount to integrate our existing knowledge on invasive plant abundance with SDM creation practices. Already studies can be highlighted that show occurrence and abundance distributional discrepancies across invasive plant species (Jarnevich, Sofaer, and Engelstad 2021; Beaury et al. 2023). Incorporating thoroughly researched invasive plant ecology dynamics into abundance-based SDMs will ensure these models are more robust and actionable as they better capture critical ecological drivers.

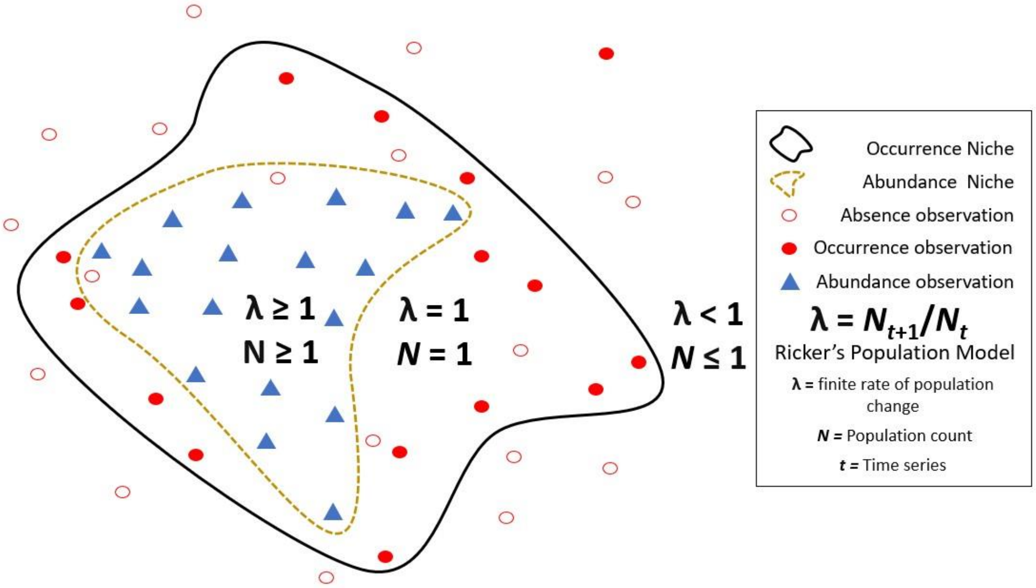

Figure 1.2 - Conceptual model depicting how a species' occurrence niche and abundance niche differ as defined by the Rickers Population Model (Rickers 1958). The area outside of the occurrence niche, defined by the space in which a species has a **K < 1**, where K is carrying capacity, and is unable to sustain an individual of that species. The area within an occurrence niche, defined by the space in which a species has **K ≥ 1**, captures a species' ability to persist. The area within the abundance niche, defined by the space in which a species population has a **K >> 1**, can sustain a population greater than one or very few individuals of the species. The abundance niche is nested within the occurrence niche but has conditions sufficiently different enough to sustain population abundance for a species.

We conducted a review of both invasive plant ecology literature and SDM literature to better inform modeling efforts regarding what factors are important for invasive plant abundance and how they can be represented in abundance-based SDMs. We will present each abundance governing factor in its own section, defining and detailing current approaches to representing these abundance governing factors within SDMs, and identifying future research directions or barriers, or both, pertaining to incorporating these factors into abundance-based SDMs. While examples of invasive plant abundance SDMs will be emphasized, these currently represent only a subset of all SDM literature. As such, when no invasive plant abundance SDMs examples are

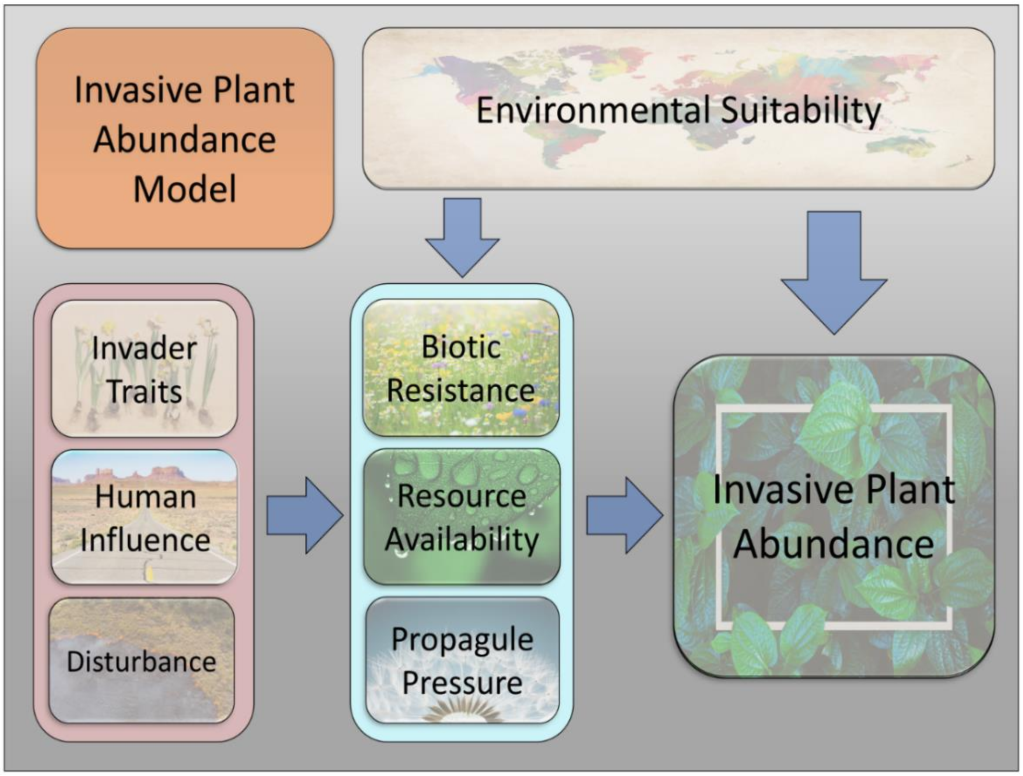

Figure 1.3 - Invasive Plant Abundance Model. Environmental Suitability, Biotic Resistance, Resource Availalbity, and Propagule Pressure all act directly on invasive plant abundance. Invader Traits, Human Influence, and Disturbance often indirectly affects invasive plant abundance by strongly influencing other governing factors. Environmental Suitability can interact with other abundance governing factors as well, exerting their overall influence on invasive plant abundance.

available, other invasive and non-invasive plant SDMs will be used to illustrate lines of evidence.

Figure 1.3 provides a visual representation of individual abundance governing factors and will serve as a "road-map" for the remainder of this paper. While this model is similar to and informed by others that depict factors controlling plant invasions (Catford, Jansson, and Nilsson 2009) or eco-physiological controls of plant distribution (Guisan and Zimmermann 2000; Mod et al. 2016; Lasky, Hooten, and Adler 2020), it differs significantly by focusing explicitly on invasive plant abundance and how these abundance governing factors may interact to determine abundance outcomes.

Environmental Suitability

Specific to this review, environmental suitability refers to the collective abiotic regime and physical characteristics of a given geographic location that determine if a study species can survive or thrive within that area. Locations that possess the requisite environmental characteristics will support the occurrence and/or abundance of a given species, while areas lacking those characteristics will not. While acknowledging a species' niche is not solely defined by abiotic elements (Grinnell 1917), predictors that fall within the category of environmental suitability, such as climate (e.g., temperature, precipitation), soil regimes (e.g., soil texture), or topographic positions (e.g., aspect, latitude/longitude), often provide exceptional controls on a species distribution.

Environmental suitability predictors are important to nearly all types of SDMs and invasive plant abundance SDMs are not an exception (Bradley et al. 2018; O'Neill, Bradley, and Allen 2021; Jarnevich, Sofaer, and Engelstad 2021; Sofaer et al. 2022). Many types of continuous climate (O'Donnell and Ignizio 2012; Senay et al. 2013) and soil (Ramcharan et al.

2018) predictor datasets that are important for species abundance are widely available and are readily leverageable for SDMs. Specific to invasive species, environmental suitability not only provides exceptionally strong controls on their establishment (Richardson, Pysek, et al. 2000; Catford, Jansson, and Nilsson 2009), but also their abundance (Rouget and Richardson 2003; Thomsen et al. 2006; Catford et al. 2011; Boulangeat, Gravel, and Thuiller 2012; Blumenthal et al. 2016; Williamson et al. 2020; Damasceno and Fidelis 2020). Environmental suitability is often one of the strongest controls on invasive plant abundance, as it not only directly inhibits or enables abundance, but it can influence other abundance governing factors (Maestre et al. 2009; Lynn et al. 2019).

While environmental suitability predictors are well explored in SDM research, one direction in particular that could benefit invasive plant abundance SDMs is consideration of geographic resolution. Geographic resolution plays an important role when utilizing environmental suitability predictors, both in terms of the resolution of the SDM itself and the resolution of the data informing the predictor. While it may be necessary to utilize coarse resolution environmental data for invasive plant abundance SDMs created at broad extents and resolutions, models seeking to have higher resolution may benefit from including predictor data capable of accounting for microclimates. Microclimates can create far more suitable habitat conditions for a species to persist (Maclean and Early 2023), and can increase invasive plant abundance within those pockets of improved environmental suitability (Song et al. 2012). The means and methods by which microclimate capturing data are collected and incorporated into SDMs are consistently improving (Lembrechts, Nijs, and Lenoir 2019) and methodological examples of their use in SDMs from other taxa are available for guidance (Illán, Gutiérrez, and Wilson 2010; Rebaudo, Faye, and Dangles 2016). Other resources for capturing microclimates in predictors may be found using downscaled climate data via topographic data sources (Wang et al. 2016). This would allow users to leverage climate data that are location specific, which provides granularity absent from climate data derived from other means, such as a gridded average approach. Greater adoption of data with resolutions capable of capturing microclimates within SDMs may provide a more complete picture of a region's environmental suitability for supporting an invasive plant abundance.

Resource availability

While resource availability is an important factor for the abundance of any plant population, it has been identified as a particularly critical factor for invasive plants (Gioria and Osborne 2014). It has even been suggested that the local resource economy can determine whether a community resists or accepts an invading plant (Pearson et al. 2018). Resource availability is defined as the quantity and accessibility of nutrients required for the survival, growth, and reproduction of plants. Categories of resources that fall under the umbrella of resource availability include sunlight, water, and other important nutrients such as nitrogen or phosphorus. While some of these types of resources may also have a relationship to environmental suitability, representing these resources in the category of resource availability differs from environmental suitability in the same way that weather differs from climate. Environmental suitability represents a mean value over time, while resource availability represents how the quantity of these resources changes over fine temporal scales due to stochastic events and heterogeneity. Higher resource availability during an invasion can result in greater invasive plant abundance (James et al. 2006; Esque et al. 2010; Liu and Kleunen 2017). Conversely, lowering resource availability of certain key resources can lower invasive plant abundance (Mazzola et al. 2011). Additionally, while long term alterations to resources regimes can result in new dynamics amongst species within a plant community that favor invasive species (Grella, Renshaw, and Wright 2018), even a limited duration of fluctuating resource availability can have lasting implications for invasive plant abundance (M. A. Davis, Grime, and Thompson 2000).

Resource availability predictors are typically represented within SDMs as predictors relating to soil nutrients or conditions. Transitory resource predictors (Piedallu et al. 2016; Walthert and Meier 2017) are important for both occurrence and abundance of invasive and native plant SDMs (Descombes et al. 2016; Mikulyuk et al. 2020; Roe et al. 2022). One study, using SDMs to predict abundance of temperate tree species across Switzerland, found that fine resolution resource availability predictors relating to soil nutrients contributed more to model performance than climatic predictors (Walthert and Meier 2017). This study is of note because habitat suitability data analysis was conducted at the individual plot level, rather than interpolated across a study region. While this approach does not result in a wall-to-wall map end-product, it does capture extremely fine resolution dynamics important to species abundance. Similar to the rationale of including microclimate data, using fine-resolution resource availability data could enhance a SDM's ability to predict invasive plant abundance. Current approaches to creating predictors relating soil resources exist at fairly fine resolutions, such as across the US at 100m resolution (Ramcharan et al. 2018) or globally at 1km resolutions via remote sensing (He et al. 2015). In addition to transitory soil resource related predictors, weather based predictors have also begun to be leveraged into animal taxa SDMs with encouraging results (Bateman, VanDerWal, and Johnson 2012; Feldmeier et al. 2018). This development has allowed for new aspects of resource availability to be incorporated into SDMs. Incorporating weather related predictors into SDMs can improve model performance by capturing short-term resource patterns that would otherwise not be detected in averaged decadal climatic data. An example specific to invasive plant abundance found that wetter fall weather patterns increased the suitability for cheatgrass abundance due to favorable germination conditions (Sofaer et al. 2022), capturing interannual variation in resources that could contribute to interannual variation in abundance of this annual species. Including types of more transitory or ephemeral resource availability predictors could better capture the importance of resource availability to invasive plant abundance and correspondingly improve abundance-based SDMs' performance.

Propagule Pressure

While certainly a driver of invasive plant occurrence (Colautti, Grigorovich, and MacIsaac 2006; Davis et al. 2016), many studies have documented propagule pressure as an important factor for invasive species abundance (Eschtruth and Battles 2009; St. Clair and Bishop 2019; Carr, Hooper, and Dukes 2019). Despite the propagule pressure's importance to invasive plants, the definition of the term is not always consistent and may change depending on the context in which it is being used (Lockwood, Cassey, and Blackburn 2009). As this review is interested specifically in invasive species abundance, the definition must include not only the movement of propagules from outside of a community to within, but also must consider the propagules produced onsite by an existing invasive plant population. Using the definition presented by Lockwood et al. (2009), we can label these dynamics as propagule pressure and propagule rain. Propagule pressure is defined as the number of propagules introduced and the frequency of introductions to a given area. Propagule rain is defined as the propagules produced by the local population. While propagule pressure does contribute to abundance, propagule rain may be a better predictor of abundance and influence where abundance occurs spatially (Rouget and Richardson 2003). Parsing whether a propagule is sourced from a local population versus a distant population is challenging given the incomplete nature of the data used to inform SDM predictors. As such, while there may be instances where there is a need to consider and differentiate the effects of propagule pressure and propagule rain, they will be considered as two parts of an individual overarching abundance governing factor that pertaining to propagules.

Despite the ecological importance of propagule pressure and propagule rain to invasive plant abundance, SDM predictors that directly capture these effects are not as common as one might hope. Other predictors highly correlated with propagule pressure and rain are more easily obtained and incorporated into SDMs. For example, human-created linear landscape features, such as roads or railways, have a positive relationship to invasive plant abundance, which can be in part explained by how these areas act as corridors that enhance propagule movement (Suárez-Esteban et al. 2016). These indirect predictors are fairly easy to obtain and incorporate into SDMs (Dullinger et al. 2009; Catford et al. 2011) and are often important for invasive species abundance (see Human Influence section). While the distinction between direct and indirect propagule pressure predictors may be academic, this becomes an important consideration when attempting to parse the degree to which human influence, disturbance, and propagule pressure are influencing invasive plant abundance. Similarly, the effects of propagule rain may be indirectly captured by accounting for factors that affect reproductive capability (e.g., resource availability, reproductive traits, or both) of the modeled species but may be unable to determine the direct importance of propagule rain on invasive plant abundance.

Fortunately, when the use of direct propagule predictors is deemed important there is a large body of literature on how to represent dispersal into SDMs. In fact, several review papers on how dispersal, movement, and landscape barriers can be incorporated into SDMs have been written exploring this topic (Franklin 2010b; Vasudev et al. 2015; Miller and Holloway 2015).

Regardless of a species' invasiveness status, dispersal is a critical consideration for SDMs predicting the range expansion or shift of a species (Elith, Kearney, and Phillips 2010). While no dispersal or unlimited dispersal is often the default assumed by many SDMs (Miller and Holloway 2015), alternative approaches may be more appropriate, especially when considering how important propagule pressure is for invasive plant abundance and how the assumption of equilibrium cannot be made when using SDMs to predict invasive species distribution (Elith 2017). Fixed dispersal (Hsu et al. 2012), mean distance to source population (Mikulyuk et al. 2020), spatial autocorrelation (Gallien et al. 2015), kernel density (A. J. S. Davis et al. 2016), or cellular automata (Merow et al. 2011) approaches can be used to represent propagule pressure/rain within SDMs with varying degrees of methodological complexity. Other factors that affect propagule pressure at large resolutions, such as landscape barriers or population demography, can also be incorporated into SDMs to further refine predictions (Franklin 2010b). Other simpler, proxy predictors for propagule pressure, such as distance to a river for riparian invasive plant SDMs (Hoffman et al. 2008; Descombes et al. 2016), can be important predictors for invasive plant abundance SDMs as well, but are dependent on the ecology of the invader. While these methodological options may be more challenging to implement, they may better capture the ecological importance direct propagule pressure/rain has on invasive plant abundance distributions.

Biotic Resistance

Biotic resistance has a long history of being recognized as an invasion inhibiting mechanism and may in fact be the first recognized barrier to invasion (Jeschke, Debille, and Lortie 2018). While initially thought of as a barrier to invasive plant occurrence (Elton 1958), evidence now suggests that biotic resistance is a more significant barrier inhibiting invasive plant abundance specifically (Levine, Adler, and Yelenik 2004; Jeschke, Debille, and Lortie 2018). The scope and context of biotic resistance has had several interpretations over the years (Jeschke, Debille, and Lortie 2018). In the context of this literature review, biotic resistance is defined as the net effects of a community's biotic interactions on invasive species abundance. Net effects is specifically included in the definition as the effects of biotic interactions on invasive plant abundance are not unidirectional. Competition (Levine, Adler, and Yelenik 2004; Mitchell et al. 2006; Braz et al. 2020; B. L. Brown and Barney 2021), herbivory (Levine, Adler, and Yelenik 2004; Mitchell et al. 2006; Suwa and Louda 2012), diseases/pathogens (Levine, Adler, and Yelenik 2004; Flory and Clay 2013; Stricker et al. 2016), facilitation (Richardson, Allsopp, et al. 2000; Mitchell et al. 2006; Pyšek et al. 2019) and other types of interactions (King and Howeth 2019; B. L. Brown and Barney 2021) all contribute to the overall net influence biotic elements have on invasive plant abundance. Each of these types of biotic resistance can be context dependent in how they affect invasive plant abundance. Competition from native species that are functionally (Jeschke and Erhard 2018; Conti et al. 2018) or phylogenetically similar (Iannone et al. 2016; Jeschke and Erhard 2018) to an invasive plant may enhance biotic resistance in some instances, but not all (Jeschke and Erhard 2018; Catford et al. 2019). Herbivory may act as a strong control on invasive plant abundance or may enhance it depending on whether the herbivory targets invasive or native species (Eschtruth and Battles 2009; Batzli and Dejaco 2013). Diseases and pathogens can enhance or diminish invasive plant abundance depending on which species act as hosts (Mitchell et al. 2006; Flory, Kleczewski, and Clay 2011; Flory et al. 2018). Furthermore, interaction between different types of biotic resistance can have synergistic effects on invasive plant abundance outcomes, such as with herbivory and competition (Center et al. 2005; Suwa and Louda 2012; Huang et al. 2012). Additionally, both the directionality and strength of certain types of biotic interactions can be strongly influenced by environmental stress gradients (Bertness and Callaway 1994; Maestre et al. 2009). While evidence suggests that biotic resistance is important in determining invasive abundance outcomes, its highly contextual and data intensive nature makes it challenging to represent within SDMs.

Given the complexity surrounding biotic resistance, representing it within SDMs can be challenging and requires careful consideration. The review paper from Dormann et al. (2018) provides a detailed list of questions modelers should consider to avoid misinterpretation or misattribution of the importance of biotic interactions within SDMs, or both. Anderson (2017) provides a framework for determining whether biotic interactions should be included as predictors within SDMs or incorporated during model post-processing, guided by whether the interaction is one affected by density dependence. Despite these nuances, many examples of biotic resistance represented within SDMs can be found. Competition is the most common type of biotic resistance found within SDMs, and can be represented in a variety of ways (Dormann et al. 2018). These approaches range in methodological complexity from using biotic resistance predictors directly (Leathwick and Austin 2001; Descombes et al. 2016), to using competition proxies such as phylogenetic diversity (Iannone et al. 2016), to creating Joint Species Distribution Models (JSDMs) depicting at least two species distribution ranges at the same time and how they influence one another (Pollock et al. 2014; Lany et al. 2018). While competition is most often the focus of biotic interactions within SDMs, research focusing on using facilitation as a model predictor does exist (Pellissier et al. 2010; Lynn et al. 2019) and can be represented in SDMs using similar methods to that of competition. Given a plethora of examples for including measurements of competition in SDMs, and the methodological similarities for facilitation, these two biotic resistance factors may be the most approachable to include within invasive plant abundance SDMs. Fewer examples exist for herbivory within plant SDMs generally and for invasive plant abundance SDMs specifically. While more data intensive approaches can be taken to represent herbivory with an SDM (Lynn et al. 2019; Castro et al. 2020), a binary herbivory presence/absence approach has been successfully incorporated into invasive plant abundance SDMs (Sofaer et al. 2022) and may represent an easily leverageable starting point for future models. Diseases/pathogens have been successfully incorporated as predictors into native plant occurrence (Kankaanpää et al. 2021) and abundance SDMs (Lynn et al. 2019), but these approaches may be limited to finer resolution models give the nature of how this type of data is collected.

While biotic resistance represents a promising avenue for invasive plant abundance SDMs to explore, meaningful barriers exist. Foremost, while biotic resistance has been found to be an important consideration for invasive plant abundance, our understanding of which types of biotic resistance matter for different invasive plants is limited. Given both the complexity of how and when different forms of biotic resistance interact with invasive plant abundance and the methodological complexity of representing these interactions in SDMs, it is not feasible to simply test all forms of biotic resistance for all invasive plant species. A good first step would be a firmer ecological understanding of what types of biotic resistance are important for different invasive plant species and when. The ecological information regarding the interactions between invasive plant species and other biotic components of a community is not sufficiently understood across all invaders. For example, while certain invasive plants may have documented interactions between competitors (Kettenring et al. 2015; Kerns and Day 2017), facilitators (Lucero et al. 2019), and herbivores (Bishop et al. 2020), such information is not ubiquitous across all invasive plants. More research on species specific interactions is needed to make the inclusion of these types of predictors more common. Even when there is strong evidence of biotic resistance, datasets containing leverageable information may simply not exist. For example, domestic cattle grazing can affect invasive plant abundance (Parks et al. 2008; Porensky, McGee, and Pellatz 2020), but datasets for domestic cattle that can be leveraged into SDMs are not readily accessible. The same can be said for many disease or pathogen datasets as well. Remote sensing represents a potentially promising avenue to address some of the gaps in biotic datasets (He et al. 2015), but cannot be leveraged for every instance of biotic resistance. Beyond knowledge and data limitations, outstanding questions involving the resolution of the SDM and the importance of biotic predictors exist. The importance of resolution and biotic interactions on a species occurrence distribution is an outstanding question across SDM research (de Araújo, Marcondes-Machado, and Costa 2014; Jenkins et al. 2020) and invasive plants are no exception. For example one study that tested the importance of overstory biotic predictors for understory invasive plant occurrence at multiple resolutions found biotic predictors were influential on SDM performance at the finest resolution tested, 1 km pixels, but no greater (Baer and Gray 2022). Given the lack of research in this area, questions surrounding the importance of biotic resistance predictors, invasive plant abundance, and SDM resolution are an area ripe for further research.

Invader Traits

Invader traits not only represent a lens through which invader community and ecosystem level impacts can be seen (Tilman et al. 1997; Mack et al. 2000; Simberloff et al. 2013), but also provide important context for determining invader abundance (Drenovsky et al. 2012; Mata, Haddad, and Holyoak 2013). Invasive plants are often found to gain advantages from their traits in their invaded range. This can be due to possessing higher trait values compared to native plants (van Kleunen, Weber, and Fischer 2010), greater plasticity found situationally amongst invasive plants (Davidson, Jennions, and Nicotra 2011), or novel traits or trait values not found within their invaded systems (Vitousek and Walker 1989). As such, while invader traits can directly alter invasive plant abundance, more often they modify other abundance governing factors in critical ways. Novel traits or superior trait values relative to the recipient community may weaken the effects of local biotic resistance (Conti et al. 2018; Catford et al. 2019). Invader traits not possessed by the recipient community may enhance resource availability by allowing an invasive plant to access resources through novel means (Brown and Rice 2010; Wolkovich and Cleland 2011; Mathakutha et al. 2019). Invader traits can also alter propagule pressure as certain propagule traits are associated with greater invader success (Uyà, Bulleri, and Gribben 2018). By interacting with these more direct abundance governing factors, invader traits can strongly alter abundance outcomes in invaded communities making them critical context for understanding invasive plant abundance.

While plant traits are not uncommon within SDM literature, they are more often used for other purposes than informing SDM predictions directly. For example, the literature on trait-based SDMs uses post-hoc regressions to explore traits-predictors relationships, using SDM accuracy metrics as a dataset to conduct this analysis (Syphard and Franklin 2010; Pollock et al. 2018; McCune et al. 2020). This approach allows researchers to ask certain questions pertaining to a trait-environment relationship but do not utilize plant traits to affect SDM performance. Most often, plant traits are used to inform model creation and can generally be categorized into one of two approaches. The first is using ecological knowledge of certain plant growth forms or life histories to select predictors during SDM creation. While selecting predictors based on ecological knowledge is a best practice for any SDM effort (Franklin 2010a), traits can help guide which predictors may be useful to include or exclude from model creation (Boulangeat, Gravel, and Thuiller 2012). The second means of including traits is by grouping species observation data by functional traits or life history characteristics such as disturbance affinity (Syphard and Franklin 2010), growth form (e.g., multi or single-stem) (Pollock et al. 2018), or habitat specialist versus generalist (Evangelista et al. 2008) and creating models for those groups of species. This approach may be particularly useful if an invasive plant species has variable growth forms.

Using plant traits to directly inform SDM predictions, not just to guide model creation, is uncommon but may provide possible future research directions for invasive plant traits and abundance predictions. Gallien et al. 2015 found that including functional traits improved their invasive plant occurrence niche models, but not abundance models, although these findings were limited to vegetation plots and not across the entirety of a study region as is the case with many SDM outputs. This methodological approach is of note as they considered invader traits in relation to the invaded communities trait values. As previously stated, the relationship between an invader's traits and the trait values of the recipient community is an important piece of context pertaining to biotic interactions. While this study did not find these traits to be an important determinant of invasive plant abundance, the invader-invaded community relational predictor approach could be a potential avenue of exploration. Remote sensing derived plant community trait data (He et al. 2015) in conjunction with invader trait values may allow for new opportunities to explore the importance of invader-invaded community relative trait values for invasive plant abundance and to do so in a way that uses a continuous predictor approach.

Disturbance

Disturbances are commonly cited as an important factor during invasions, but their effect on invader abundance can be variable (Hobbs and Huenneke 1992; Price et al. 2011; Kettenring et al. 2015; Damasceno and Fidelis 2020). Disturbance is defined by White and Picket 1985 as "…any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment". Given the broad nature of this definition, it should not come as a surprise that effects of disturbance on invader abundance are highly contextual (Nordheimer and Jeschke 2018). Disturbance type (Jauni, Gripenberg, and Ramula 2015), severity (Eschtruth and Battles 2009; Kerns and Day 2017; Daniels and Larson 2020), extent (Britton-Simmons and Abbott 2007), frequency (Lonati et al. 2009), time since disturbance (Abella and Springer 2015; Manning et al. 2018; Damasceno and Fidelis 2020), and departure from historical disturbance regime (Moles et al. 2012) all play important roles in determining the net effect of a disturbance on invasive plant abundance. While disturbances themselves can alter invasive plant abundance in the short term, such as via the Allee effect (Stephens, Sutherland, and Freckleton 1999; Buckley, Bolker, and Rees 2007), often the true effect of disturbance on invader abundance is a function of its interaction with primary abundance governing factors (Figure 1.3) (Moles et al. 2012). Disturbances can alter local biotic interactions (Kettenring et al. 2015), enhance resource availability (Esque et al. 2010), and create new opportunities for invader propagules to germinate (Spence et al. 2011; Driscoll et al. 2016; Emsweller et al. 2018). Finally, invasive plants can themselves alter disturbance regimes. This process can create feedback loops where a disturbance regime altered by an invasive plants' abundance will result in conditions that favor that invasive plant, allowing for the disturbance-invader cycle to perpetuate (Aslan and Dickson 2020; D'Antonio and Vitousek 1992).

In the context of SDMs, disturbances are often readily leverageable given their spatial nature. Covariates relating to fire are common in SDMs, as there is often a strong assumed relationship between fire and invasive plants, and fire related data are often easy to obtain and include in SDMs. Fire extent (Sofaer et al. 2022) and fire frequency (Jarnevich, Sofaer, and Engelstad 2021) have both been important predictors for invasive plant abundance SDMs. Fire severity (Mahood, Koontz, and Balch 2023) and fire return intervals (Magadzire et al. 2019) have yet to be tested for invasive plant abundance, but examples of successfully incorporating covariates representing these disturbance characters can be found in the literature for native and invasive plant occurrence SDMs. Alternative approaches to using predictors to represent disturbance may also be used, such as comparing predictions across models using species occurrence points from burned and unburned areas (Peeler and Smithwick 2018). While fewer examples of flood related predictors are available, there do exist examples in the literature. Riverine disturbances in the form of predictors relating to erosion have also been found to improve invasive plant abundance SDMs (Descombes et al. 2016). These erosion predictors can be calculated via Geographic Information System (GIS) software (le Roux, Virtanen, and Luoto 2013), making them relatively low cost. Finally, canopy cover change can be captured and parameterized for SDMs via remote sensing products (Schwantes, Swenson, and Jackson 2016), allowing events such as hurricanes or drought to be included in abundance-based SDMs to explore their effects on invasive plant abundance.

Human Influence

The final abundance governing factor is human influence. Human influence encompasses all direct and indirect effects human activities have on an ecosystem. This is a necessarily broad definition as the ways in which human activities affect ecosystems are numerous. Human influences on a landscape may range from obvious to highly obscured. For example, on the obvious and direct end of the spectrum is the conversion of a swamp to agricultural lands, while on the obscured and indirect end are changes to precipitation regimes induced by anthropogenic climate change. Despite how different these human driven changes to an ecosystem may be, each may have significant implications for invasive plant abundance. This is because human activities have well-documented, strong interactive effects with nearly all invasive plant abundance governing factors (Catford, Jansson, and Nilsson 2009). While human influence can directly affect invasive plant abundance, such as actively planting or removing invasive plants, indirect interactions via modifying other abundance governing factors is far more common. Intermediate levels of human influence cultivate an ideal environment for invasive plants by altering biotic communities, enhancing resource availability, and creating pathways for propagules (Zimmermann et al. 2014; Cadotte et al. 2017; Gaertner et al. 2017). This bears out in studies that show human population centers, both large (Pysek et al. 2010) and small (McLean et al. 2017), are highly correlated with invasive plant abundance. Transportation corridors also have a positive correlation with invasive plant abundance (Suárez-Esteban et al. 2016), as they too alter landscape conditions to be more favorable for invasive plants.

In addition to the ecological importance of human activity on invasive plant abundance, the explicit spatial nature of these activities makes them easier to include and leverage for invasive plant abundance-based SDMs. Human influence related predictors are commonly important for invasive plant abundance-based SDMs (Descombes et al. 2016; Jarnevich, Sofaer, and Engelstad 2021; Sofaer et al. 2022). Human influence predictors are commonly represented by either distance to transportation corridors (Simpson and Prots 2013; Sittaro, Hutengs, and Vohland 2023) or distance to population centers (Simpson and Prots 2013; Bazzichetto et al. 2021). These are exceedingly common ways to represent human influence because of both ready accessibility and the strong relationship they have with invasive plant abundance. Human modification models (Kennedy et al. 2019) that can serve as a proxy for degree of human impact have also been used in invasive plant abundance-SDMs and have been important predictors (Jarnevich, Sofaer, and Engelstad 2021). Less common, but potentially just as beneficial, are measures of remoteness (Bazzichetto et al. 2021). Remoteness predictors can indicate how challenging it can be to reach a given area for humans, indicating some degree of how likely that area is to be subject to human influence and to what degree. While more challenging to create, remoteness could offer a new predictor for predicting invasive plant abundance on the landscape.

Table 1.1: Summary table identifying each category of invasive plant abundance governing factor, why that factor influences invasive plant abundance, examples of how that factor is represented or accounted for within SDMs, and future research directions or recommendations pertaining to how to better incorporate these factors into SDMs.

Abundance Governing Factor	Ecological Relevance to Invader Abundance	Covariate or Method Example	Future Research Direction or Recommendations
Environmental Suitability	Environmental regimes that constrain the abundance of an invasive plant due to physiological requirements and adaptations (Franklin 2010a)	Continuous temperature and precipitation predictors (Jarnevich, Sofaer, and Engelstad 2021) Non-transitory soil predictors (Jarnevich, Sofaer, and Engelstad 2021)	Microclimate predictors (Lembrechts, Nijs, and Lenoir 2019) Downscaled climate data (Wang et al. 2016)
Resource Availability	Resources available to an invasive plant that are utilized for growth and reproduction. (Gioria and Osborne 2014)	Transitory soil predictors (Piedallu et al. 2016; Walthert and Meier 2017) Interpolated weather data (Sofaer et al. 2022)	Interpolated model for fine resolution transitory soil predictors (Ramcharan et al. 2018) Remote sensing derived fine resolution transitory soil predictors (He et al. 2015;

			O'Donnell and Manier 2022)
Propagule Pressure/ Propagule Rain	Propagule Pressure – The number of propagules introduced and the frequency of introduction to a given area (Lockwood, Cassey, and Blackburn 2009). Propagule Rain – The propagules produced by the local population (Lockwood, Cassey, and Blackburn 2009) Propagule pressure and propagule rain combine to determine the number of opportunities to produce new individuals within an invasive plant population.	No dispersal/unlimited dispersal assumption (Miller and Holloway 2015) Distance to waterway (Hoffman et al. 2008; Descombes et al. 2016) Fixed dispersal rate (Miller and Holloway 2015) Spatial autocorrelation (Gallien, Carboni, and Münkemüller 2014) Kernel density (A. J. S. Davis et al. 2016) Cellular automata (Merow et al. 2011) Dispersal models or indexes (Havel, Shurin, and Jones 2002; Boulangeat, Gravel, and Thuiller 2012; A. J. S. Davis et al. 2016)	Moving beyond assumption of no dispersal/unlimited dispersal assumption or at least including a justification of why that assumption is being made (Miller and Holloway 2015)
Biotic Interactions	Net effect that a recipient community's biotic elements have on invasive species	Competition (Leathwick and Austin 2001; Pollock et al. 2014;	General improved ecological understanding of

	abundance, of which multiple sources can contribute (Levine, Adler, and Yelenik 2004) Representing biotic interactions within SDMs can be complex and requires consideration to ensure the effects of biotic interactions on a species distribution are not misrepresented (Anderson 2017; Dormann et al. 2018)	Descombes et al. 2016; Lany et al. 2018) Facilitation (Pellissier et al. 2010; Lynn et al. 2019) Phylogenetic diversity (Iannone et al. 2016) Herbivory (Lynn et al. 2019; Castro et al. 2020; Sofaer et al. 2022) Disease/Pathogens (Lynn et al. 2019; Kankaanpää et al. 2021)	invader biotic interactions Improved aggregation of data/ data collection efforts to create herbivory, disease/pathogens, and landscape connective predictors May only be appropriate to use in SDMs that use sufficiently fine resolutions (Baer and Gray 2022)
Invader Traits	Functional traits of an invasive plant in relation to the recipient community allows enhanced or diminished competitive ability, resource capture, or reproductive advantage (van Kleunen, Weber, and Fischer 2010; Mathakutha et al. 2019).	Post-hoc regressions (Pollock et al. 2018; McCune et al. 2020) Predictor selections based on species life history and growth form (Beaury et al. 2023) Invader-invaded community relative trait values (Gallien et al. 2015)	Invader-invaded community relative trait values as continuous predictors, derived from remote sensing
Disturbance	Disturbance can increase or decrease invader abundance by altering local biotic	Fire - extent (Sofaer et al. 2022), frequency (Jarnevich, Sofaer, and Engelstad 2021),	Remotely sensed land cover change

	and resource dynamics or through the movement of propagules, or both. A disturbance's effect on abundance is also highly dependent on its attributes (Hobbs and Huenneke 1992).	severity (Mahood, Koontz, and Balch 2023) return interval (Magadzire et al. 2019) Riverine disturbances (Descombes et al. 2016)	(Schwantes, Swenson, and Jackson 2016)
Human Influence	Intermediate levels of human influence cultivate an ideal environment for invasive plant abundance by altering biotic communities, enhancing resource availability, and the creation of pathways for propagule pressure (Zimmermann et al. 2014; Cadotte et al. 2017; Gaertner et al. 2017).	Distance to population centers (Simpson and Prots 2013; Bazzichetto et al. 2021) Distance to roads (Mikulyuk et al. 2020) or transportation corridors (Sittaro, Hutengs, and Vohland 2023) Human Modification Model derived predictor (Kennedy et al. 2019)	Predictors capturing remoteness (Bazzichetto et al. 2021)

Discussion

This is not the first review to say that we need to consider a greater variety of covariates with SDMs (Mod et al. 2016). Nor is it the first review to look at invasive plant abundance as a function of system-level interactions (Gallien and Carboni 2017). But the importance of merging these two concepts is paramount. As we begin to more heavily utilize SDMs for research, management, and policy making applications (Sofaer et al. 2019), it is critical that our models reflect real world ecological dynamics. The documented relationship each abundance governing factor has with invasive plant abundance and the frequent absence of these factors from abundance-based SDMs suggests that we may be missing vital information from our models. It is entirely possible that even our well performing abundance-based models are missing critical predictors that capture ecological controls for invasive plant abundance, providing us with an incomplete picture of invasive plant abundance distributions. Many different methodological approaches on how to best represent abundance governing factors within abundance-based SDMs have been explored to date, reducing some of the barriers to including these predictors in our models (Table 1.1).

The findings of this review suggest that abundance-based invasive plant SDMs can be improved by incorporating a greater number of abundance governing factors, but doing so is not always straightforward. While many abundance governing factors have unique challenges associated with being incorporated into a SDM (Table 1.1), there are generalizations we can make about what those limitations and barriers are and how to address them. First, while abundance governing factors in SDMs are discussed here in general terms, the ecology of the modeled species is of the utmost importance for determining what abundance factors should be included. The ecological relevance of any given abundance governing factor is subject to change from invasive species to invasive species. For example, one study that created many different abundance SDMs found that the inclusion of biotic interactions and propagule pressure did not improve model performance equally for every species (Boulangeat, Gravel, and Thuiller 2012). This suggests a greater need for research regarding the ecology of specific invasive plant species to better select relevant predictors. Second, the resolution of the data used to create abundance-based SDM predictors needs to be sufficiently fine to capture dynamics important to invasive plant abundance. The importance of abundance governing factors can change along with the resolution of a SDM (K. A. Brown, Spector, and Wu 2008; Loo et al. 2009; Cabra-Rivas et al. 2016; Baer and Gray 2022) and thus the predictors representing these governing factors need to be at an appropriate resolution. A critique common within SDM literature pertaining to climatic predictors is that they can be too coarse in terms of spatial or temporal resolution and thus not matching the scale of ecological relevance (Gardner, Maclean, and Gaston 2019). Ensuring that model predictors are ecologically relevant in terms of spatial and temporal resolution is important to most types of predictors representing abundance governing factors. Third, the use of certain types of data or methodological approaches to create certain types of predictors may be required. For example, joint-SDMs may be required to accurately capture biotic interactions (Lany et al. 2018) or an approach using Bayesian hierarchical models (De Rivera et al. 2019) may be required to deal with predictor-derived models created using very different methodologies. These approaches have an inherent tradeoff though, as they may be more optimal for creating accurate models but may create technical challenges for researchers or interpretability hurdles for end users (Sofaer et al. 2019). Finally, in addition to the barriers identified above, data limitations were consistently identified as a challenge for SDMs. Datasets that contain relevant data, at relevant resolutions, that can be included in SDMs are often lacking across abundance governing factors. This creates significant challenges when a certain factor is known to be highly important for invasive plant abundance but cannot be included in model creation because of a lack of data. While proxies can be used, such as using Horse and Burro Management Areas (HMAs) to create a binary presence/absence predictor for herbivory (Sofaer et al. 2022), often the ability to create proxies is either cumbersome or non-feasible. It is critical to be able to represent ecologically important factors that influence invasive plant abundance within abundance-based SDMs, and that starts with making data more accessible for researchers.

While representing every aspect of all abundance governing factors is not realistic or even possible, the overarching theme of this review is that invasive plant abundance-based SDMs stand to benefit from the inclusion of a greater number of abundance governing factors. These benefits can be seen both quantitatively, by improving the model performance metrics, and conceptually, by better capturing the ecological reality of an invasive plant and its environment. Abundance-based SDMs that perform better and have a stronger conceptual underpinning are not only more useful, but they will be easier to explain to end users and have a degree of credibility if the model inputs are consistent with what is known to be ecologically relevant to a given invasive plant. By better integrating invasive plant ecology knowledge into abundance-based SDMs, more credible, higher performing models can be created to research, manage, and make decisions regarding invasive plants.

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CHAPTER 2 - THE IMPORTANCE OF BIOTIC INTERACTIONS FOR INVASIVE PLANT ABUNDANCE-BASED SPECIES DISTRIBUTION MODELS: A CASE STUDY USING CHEATGRASS (*BROMUS TECTORUM*)

Introduction

Invasive plants are a wide-spread ecological and economic problem. When abundant, invasive plants can reduce native community diversity, impair ecosystem function, and alter beneficial ecosystem services (Mack et al. 2000). As such, the ability to predict where and when an invasive plant population can become abundant is important for invasive plant management and decision making. Abundance-based species distribution models (SDMs) are often used for this purpose. Abundance-based SDMs can predict the suitability of a given area to support invasive plant abundance by considering a range of predictors such as climatic conditions, soil attributes, and landscape context (Jarnevich et al. 2021, Sofaer et al. 2022, Beaury et al. 2023).

SDMs are typically focused on environmental suitability broadly, but there are many additional local scale factors that influence invasive plant abundance (Teich et al In Review). Biotic interactions (BI), defined as the positive or negative interaction between species that influence population abundance, play a well-documented role in the abundance of invasive

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plants. For example, in one meta-analysis, biotic interactions in the form of native plant competition consistently reduced the abundance or performance of invasive plants (Levine et al. 2004). Despite their documented influence on invasive plant abundance, biotic interactions can be challenging to represent in SDMs for a variety of reasons. These include a lack of research regarding important species to species interactions, insufficient availability of continuous predictor data capable of representing important biotic interactions, or challengingly complex conceptual/methodological modeling approaches (Anderson 2017, Dormann et al. 2018). While acknowledging the challenges surrounding the representation of biotic interactions within SDMs, there are successful examples of their inclusion. Biotic interactions are important for both invasive plant occurrence distributions (Gallien et al. 2015, Bazzichetto et al. 2021, Baer and Gray 2022) and native plant abundance distributions (Elmendorf and Moore 2008, Boulangeat et al. 2012, Lynn et al. 2019). What has yet to be tested though, is the importance of biotic interactions for invasive plant abundance distributions. Furthermore, the environmental context in which biotic interactions are important for abundance-based SDMs is also unknown. Interactions between species that alter abundance can be strongly influenced by environmental gradients (Boulangeat et al. 2012). Understanding how environmental conditions influence species to species interactions would provide additional context regarding the controls on invasive plant abundance distributions.

Competition (Levine et al. 2004, Braz et al. 2020) and facilitation (Lucero et al. 2019) from other plant species are commonly identified as important for invasive plant abundance and have been important for plant distributions in other SDM studies (Boulangeat et al. 2012, Baer and Gray 2022). This makes competition and facilitation a logical starting point to explore the importance of biotic interactions for invasive plant abundance distributions.

We ask the questions, “Do biotic interactions in the form of competition and facilitation help explain invasive plant abundance distributions and does the environmental context in which these interactions occur matter?” To investigate this, we explored how using competition and facilitation in conjunction with abundance-based SDM predicted environmental suitability alter the probability of cheatgrass (*Bromus tectorum*) abundance. We created generalize linear models (GLMs) for low, medium, and high cheatgrass abundance that used SDM derived environmental suitability and the aggregate cover value of plant functional groups to determine if and when the inclusion of biotic variables improved the explanatory power of these models. We expected to find that biotic interactions would be important for medium and high cheatgrass abundance, but the degree to which biotic interactions are important for all abundance models will be dependent on environmental suitability.

Methods

Species Selection

Cheatgrass is an invasive winter annual grass with a highly generalist nature, and its invaded range spans the western United States (Knapp 1996). This species impacts ecosystems by altering plant community structure and significantly changing historical fire regimes (Chambers et al. 2007, Germino et al. 2015). Studies have demonstrated that cheatgrass cover is negatively influenced by perennial graminoids (Reisner et al. 2013, Chambers et al. 2016, Kerns and Day 2017), trees under certain environmental conditions (Chambers et al. 2016), and annual forbs (Kerns and Day 2017). Alternatively, cheatgrass cover can be positively influenced by shrubs (Chambers et al. 2007, 2016). Cheatgrass abundance observations are numerous across many datasets, including the Bureau of Land Management’s (BLM’s) Assessment, Inventory, and Monitoring (AIM) Landscape Management Framework database (Bureau of Land Management

2022). The AIM dataset contains plot level data including point line intercept transects that can be used to calculate percent cover for encountered plant species. This data structure allows us to ask questions pertaining to the biotic interactions of cheatgrass and other co-occurring plant species.

Species Observations

We aggregated cheatgrass abundance observations from several sources containing invasive plant locations (Table S1). These sources included: the Early Detection and Distribution Mapping System (EDDMapS) (EDDMapS 2023), the Bureau of Land Management's (BLM) Assessment, Inventory and Management (AIM) (Bureau of Land Management 2022), the BLM (Reitsma 2021) and National Park Service's (NPS) (NPS 2023) National Invasive Species Information Management System (NISIMS), an aggregated dataset containing cover values for plants from Beaury et al. 2023, the Standardized Plant Community with Introduced Status (SPCIS) database (Petri et al. 2023), and the LANDFIRE reference database (LANDFIRE 2016) (see Table S1 for additional details).

We used the Integrated Taxonomic Information System (ITIS; www.itis.gov) as an authoritative taxonomy to obtain all synonyms for cheatgrass using the R package "taxize" (Chamberlain et al. 2020). We then filtered records to only contain observations from 1980 or later to retain only temporally relevant observations. Species observations were flagged if they contained known common coordinates issues in biological collection databases using the R package "CoordinateCleaner" (Zizka et al. 2019). We also removed records with coordinates errors such as observations located in oceans, coordinates with latitude and longitudes equal to zero, and species with equal latitude and longitude coordinates.

We classified each observation record with a quantitative measurement of cover into high abundance (+50% cover), medium abundance (+25-50% cover), or low abundance (5-25% cover). When numeric percent cover metrics were not reported, we assigned each qualitative description into a category of abundance: low = “low”; medium = “medium”, “moderate”, “common”, “patch”, “patchy”, “scattered dense patches”; high = “high”, “dense”, “abundant”, “heavy”, “major”, “dense monoculture”, “dominant cover”. AIM data was kept separate prior to spatial thinning as they were used for post model fitting analyses. We spatially thinned the categorized abundance observations to 5-km to reduce spatial bias, preferentially retaining the largest category of abundance, using the “spThin” package (Aiello-Lammens et al 2015). This resulted in n = 6877 for low abundance, n = 3855 for medium abundance, and n = 1712 for high abundance for training data in fitting SDMs. We used the withheld AIM data for model testing and assessing BI importance, totaling n = 4265 for low abundance, n = 2325 for medium abundance, and n = 1402 high abundance spatially thinned locations. Along with using the AIM data as an independent data set for model assessment, we implemented 9-fold spatial block cross-validation (CV) to assess model sensitivity to the dataset used to train the model.

Background Point Generation

Because we did not have absence data, we created background points to use in model fitting using a previous established workflow (Young et al. 2020). We constrained the extent for background points using a previously generated 99% binary kernel density estimation (KDE) surface for *Bromus tectorum* that was derived from the set of abundance observations. For test background locations, we obtained a BLM land surface area management polygon layer (Bureau of Land Management 2023) and used it to define the area in which to generate background points because AIM plots are distributed across BLM lands. This process was repeated for each category of abundance, resulting in 10,000 testing and training background points for low, medium, and high abundance.

SDM Predictors

We initially considered a set of predictors (n = 53) representing climatic, soil, and landscape factors at a 90 m^2 spatial resolution (Jarnevich et al. 2021). We selected a subset based on life history and ecological knowledge of *Bromus tectorum.* For each category of abundance, we further reduced the covariates by selecting one of any pairs with a correlation coefficient >|0.7| (Dormann et al. 2013). Retained predictors for each model can be found in Table S2.

SDM Creation and Evaluation

We fit all models using the VisTrails Software for Assisted Habitat Modeling package (Morisette et al. 2013) using five algorithms: Boosted Regression Trees (BRT), Generalized Linear Models (GLM), Multivariate Adaptive Regression Splines (MARS), Maxent, and Random Forests (RF). When the training area under the receiver operating characteristic curve (AUC) or CV mean AUC were below 0.7, we optimized algorithm specific parameters for that model (Table 1.2). We assessed model performance was using the independent test data associated with the modeled abundance level. We calculated model evaluation metrics including training, CV mean, and test AUC as well as Continuous Boyce Index (CBI). We created an ensemble using any of the five algorithms with CBI values > 0.5 for each of the levels of abundance by calculating the mean relative suitability value, hence forth referred to as environmental suitability. Environmental suitability, a metric ranging from 0.0 to 1.0 that characterizes relative suitability at a given location for the modeled abundance level, for every AIM plot location containing *Bromus tectorum* abundance observations. These environmental suitability values were used for further analysis detailed below.

Biotic Variables

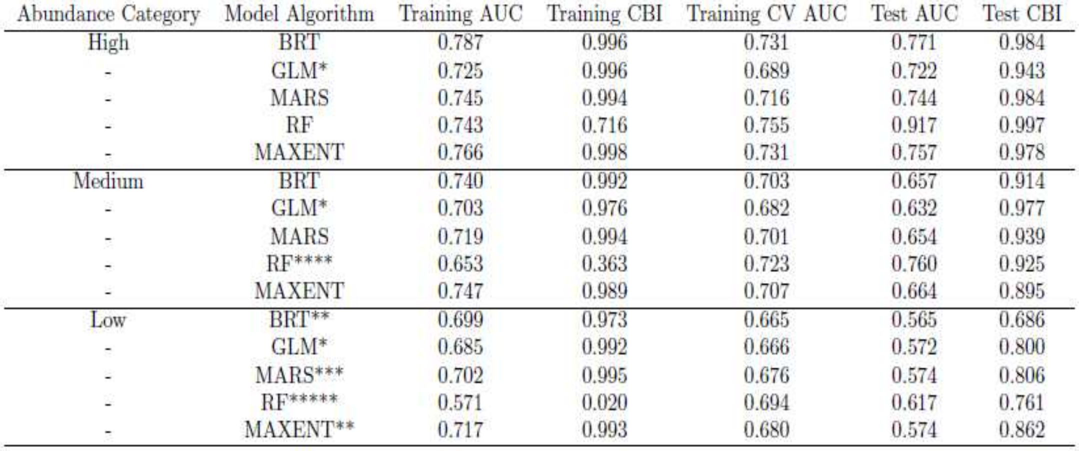
To represent the biotic interactions of competition and facilitation within this study, we aggregated cover values across different categories of growth form and duration when applicable. To this end, we selected AIM plots containing *Bromus tectorum* cover data, resulting in 11,708 observations. Using the USDA plants database (NRCS 2024), we assigned duration (annual, biennial or perennial) and growth form (graminoid, forb, subshrub, shrub, tree, and vine) to all species recorded in any of these AIM plots. We calculated cover for each grouping of growth form and duration. It should be noted that as we are grouping cover values for growth forms, this number can exceed 100.

Statistical Analysis

Given the structure of the data, e.g., all AIM data received a binary classification for each category of abundance, we used a generalized linear model (GLM) with a logit link to analyze the data, the output of which is a 0.0 through 1.0 probability of cheatgrass abundance. We fit GLMs using categories of abundance as the dependent variable and the biotic variables and environmental suitability as independent variables using forward and backward stepwise reduction of model predictors. We transformed biotic variables using log +1 for normality. We compared independent variables in the GLMs for collinearity and each instance of collinearity the more ecologically relevant variable was retained. We calculated Tjur's R^2 for each GLM as a way to display the explanatory ability of each model (Tjur 2009). For each category of abundance, we also compared models containing environmental suitability and biotic variables to models containing environmental suitability only. We used ANOVA models with Chi-squared tests to determine if environmental suitability only models were statistically different from models also including biotic variables. Finally, we plotted GLM predictions of the probability of cheatgrass abundance and significant interaction of environmental suitability and biotic variables. The values used for biotic variable in these plots were represented minimum and maximum cover values across the dataset to illustrate the effects biotic variables may have on cheatgrass probability.

Results

Table 2.1: Summary of model evaluation metrics for each category of abundance and type of algorithm. *Can't optimize GLM. ** Optimizing did not improve *** Optimization: MarsPenalty = 3.0, MarsDegree = 2. **** Removed for further analysis due to substandard performance.

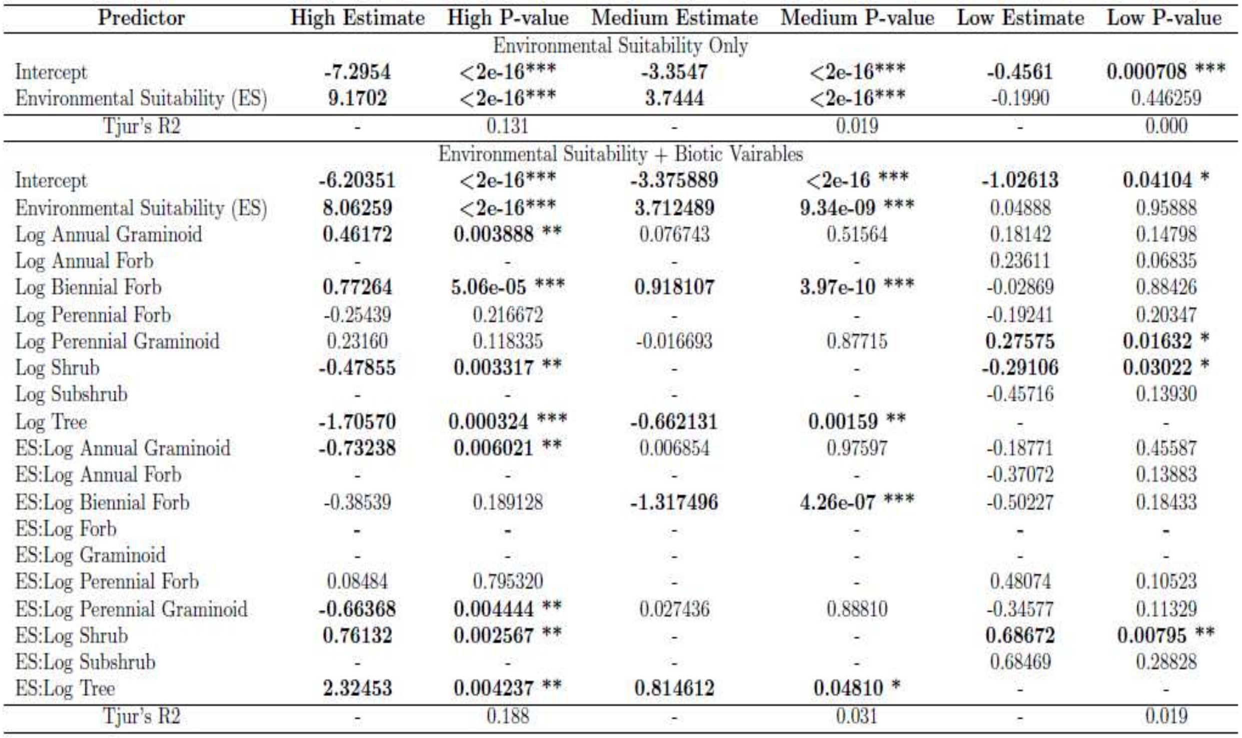


Abundance Category	Model Algorithm	Training AUC	Training CBI	Training CV AUC	Test AUC	Test CBI
High	BRT	0.787	0.996	0.731	0.771	0.984
-	GLM*	0.725	0.996	0.689	0.722	0.943
-	MARS	0.745	0.994	0.716	0.744	0.984
-	RF	0.743	0.716	0.755	0.917	0.997
-	MAXENT	0.766	0.998	0.731	0.757	0.978
Medium	BRT	0.740	0.992	0.703	0.657	0.914
-	GLM*	0.703	0.976	0.682	0.632	0.977
-	MARS	0.719	0.994	0.701	0.654	0.939
-	RF****	0.653	0.363	0.723	0.760	0.925
-	MAXENT	0.747	0.989	0.707	0.664	0.895
Low	BRT**	0.699	0.973	0.665	0.565	0.686
-	GLM*	0.685	0.992	0.666	0.572	0.800
-	MARS***	0.702	0.995	0.676	0.574	0.806
-	RF*****	0.571	0.020	0.694	0.617	0.761
-	MAXENT**	0.717	0.993	0.680	0.574	0.862

Models for high abundance performed very well across all metrics, but especially for CBI (test CBI > 0.943; Table 2.1). For medium abundance models, test CBI overall performed slightly worse than high abundance models but still well (test CBI range 0.895 to 0.977). Test CBI across low abundance models performed more poorly than high or medium abundance, ranging from 0.686 to 0.862 test CBI. Medium and low RF training CBI performed well under 0.500 and not included in the ensembles used for further analysis.

For each category of abundance, environmental suitability + BI models outperformed environmental suitability only models (Table 2.2). Environmental suitability + BI models outperformed environmental suitability only models with Tjur's R^2 values of 0 to 0.018 for low, 0.019 to 0.036 for medium, and 0.131 to 0.188 for high abundance. These differences were also significantly different ($p<0.05$) (Table S3).

Table 2.2 : GLM summary table for low (5-25% cover), medium (>25%-50 cover) and high (>50% cover) for *Bromus tectorum*. ES is abbreviated for Environmental Suitability. " : " denotes variable interactions. Statistically significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05



Predictor	High Estimate	High P-value	Medium Estimate	Medium P-value	Low Estimate	Low P-value
			Environmental Suitability Only			
Intercept	**-7.2954**	**<2e-16*****	**-3.3547**	**<2e-16*****	**-0.4561**	**0.000708 *****
Environmental Suitability (ES)	**9.1702**	**<2e-16*****	**3.7444**	**<2e-16*****	-0.1990	0.446259
Tjur's R2	-	0.131	-	0.019	-	0.000
			Environmental Suitability + Biotic Vairables			
Intercept	**-6.20351**	**<2e-16*****	**-3.375889**	**<2e-16 *****	**-1.02613**	**0.04104 ***
Environmental Suitability (ES)	**8.06259**	**<2e-16*****	**3.712489**	**9.34e-09 *****	0.04888	0.95888
Log Annual Graminoid	**0.46172**	**0.003888 ****	0.076743	0.51564	0.18142	0.14798
Log Annual Forb	-	-	-	-	0.23611	0.06835
Log Biennial Forb	**0.77264**	**5.06e-05 *****	**0.918107**	**3.97e-10 *****	-0.02869	0.88426
Log Perennial Forb	-0.25439	0.216672	-	-	-0.19241	0.20347
Log Perennial Graminoid	0.23160	0.118335	-0.016693	0.87715	**0.27575**	**0.01632 ***
Log Shrub	**-0.47855**	**0.003317 ****	-	-	**-0.29106**	**0.03022 ***
Log Subshrub	-	-	-	-	-0.45716	0.13930
Log Tree	**-1.70570**	**0.000324 *****	**-0.662131**	**0.00159 ****	-	-
ES:Log Annual Graminoid	**-0.73238**	**0.006021 ****	0.006854	0.97597	-0.18771	0.45587
ES:Log Annual Forb	-	-	-	-	-0.37072	0.13883
ES:Log Biennial Forb	-0.38539	0.189128	**-1.317496**	**4.26e-07 *****	-0.50227	0.18433
ES:Log Forb	-	-	-	-	-	-
ES:Log Graminoid	-	-	-	-	-	-
ES:Log Perennial Forb	0.08484	0.795320	-	-	0.48074	0.10523
ES:Log Perennial Graminoid	**-0.66368**	**0.004444 ****	0.027436	0.88810	-0.34577	0.11329
ES:Log Shrub	**0.76132**	**0.002567 ****	-	-	**0.68672**	**0.00795 ****
ES:Log Subshrub	-	-	-	-	0.68469	0.28828
ES:Log Tree	**2.32453**	**0.004237 ****	**0.814612**	**0.04810 ***	-	-
Tjur's R2	-	0.188	-	0.031	-	0.019

A combination of environmental suitability and biotic variables significantly predicted cheatgrass abundance (Table 2.2). High and medium cheatgrass abundance was predicted by environmental suitability, however, low abundance was not. Perennial graminoid cover was positively associated with low cheatgrass abundance probability, while shrub cover was negatively associated. Biennial forb cover was positively associated with medium cheatgrass abundance probability, while tree cover was negatively associated with medium cheatgrass abundance probability. Annual forb cover and biennial forb cover were both positively associated with high cheatgrass abundance. Tree cover and shrub cover were negatively associated with high cheatgrass abundance probability.

We also observed several significant interactions in which the effects of biotic interactions depended on our estimate of environmental suitability (Table 2.2). Shrub cover interacted with environmental suitability to increase the probability of cheatgrass at low abundance (Figure 2.1). Although shrub cover negatively affected low cheatgrass abundance probability when suitability was low, above 0.50 environmental suitability shrub cover dramatically increases the probability of low cheatgrass abundance probability. Medium cheatgrass abundance was also affected by the interaction of biotic variables and environmental suitability (Figure 2.2). Biennial forb cover positively influenced the probability of medium cheatgrass abundance when environmental suitability was very low, but as environmental

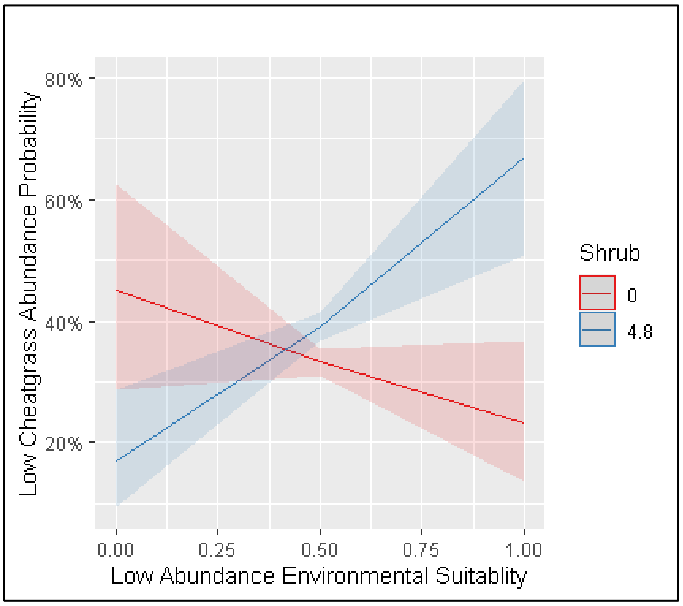


Figure 2.1: The interaction of environmental suitability with shrub cover on low cheatgrass abundance (5-25% cover). The two lines denote the minimum (0) and maximum (4.8) shrub cover values used in the analysis.

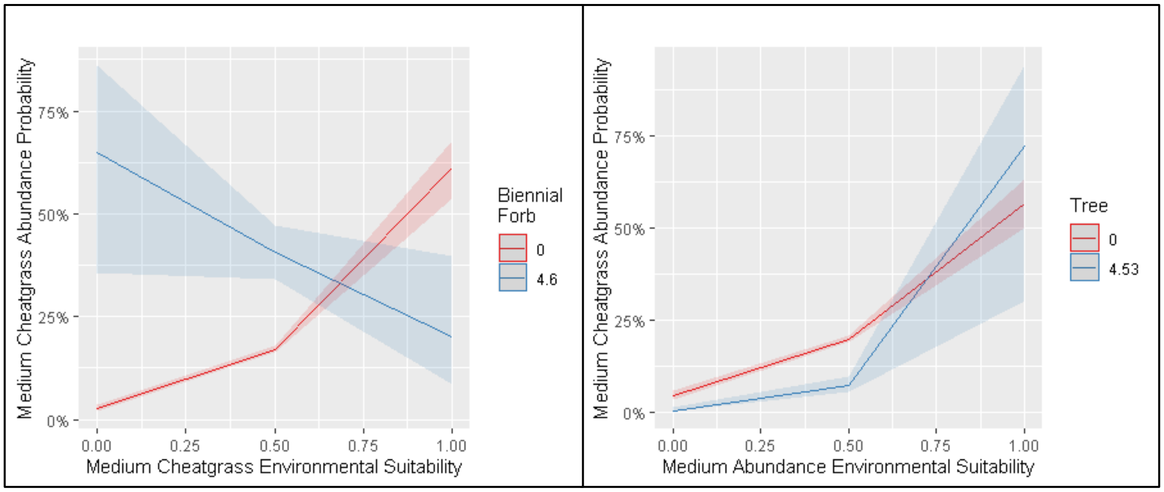


Figure 2.2 : The effects of interactions of environmental suitability and biotic variables on medium (+25-50%) cheatgrass abundance probability. The two lines in each graph represent the minimum and maximum cover values for each biotic variable used in the analysis. Top - Environmental Suitability with minimum (0) and maximum (4.6) Biennial Forb cover. Bottom - Environmental Suitability with minimum (0) and maximum (4.53) Tree cover.

suitability increased this effect on medium cheatgrass abundance probability was diminished. Conversely, tree cover negatively influenced medium cheatgrass abundance probability when environmental suitability was below 0.50 but as environmental suitability increased the effect tree cover had on medium cheatgrass abundance became negligible.

The interaction of environmental suitability and biotic predictors had even stronger effects on the probability of high cheatgrass abundance (Figure 2.3). When environmental suitability exceeded 0.50, high cheatgrass abundance probability was consistently lower when accounting for perennial graminoid cover. Conversely, shrub cover positively influences high cheatgrass abundance probability when environmental suitability was high. At low environmental suitability, the absence of tree cover resulted in marginally greater high cheatgrass probability, but this effect was diminished as environmental suitability increased.

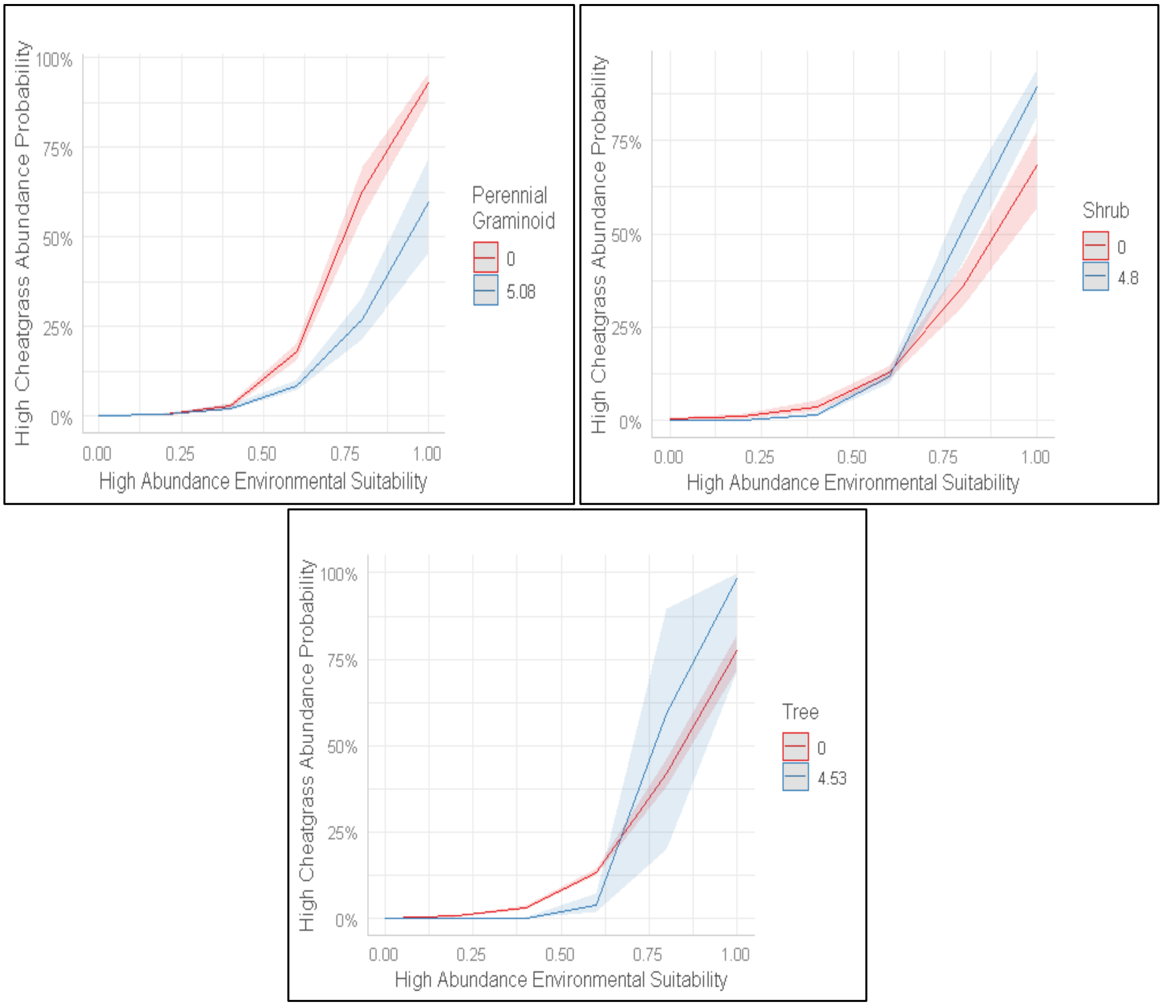


Figure 2.3: The effects of the interaction between environmental suitability and biotic variables high (+50%) cheatgrass abundance probability. The two lines on each graph represent the minimum and maximum cover value for each biotic variable used in the analysis. Left- High Abundance Environmental Suitability with minimum (0) and maximum (5.08) Perennial Graminoid cover. Right – High Abundance Environment Suitability and minimum (0) and maximum (4.8) Shrub cover. Center – High Abundance Environmental Suitability and minimum (0) and maximum (4.53) Tree cover.

Discussion

Our study demonstrates that accounting for biotic variables representing competition and facilitation alongside environmental suitability can substantially improve our ability to predict where an invasive plant, in this case cheatgrass, can become abundant. These findings align with the conclusions of other studies focused on invasive plant occurrence-based SDMs (Gallien et al.

2015, Bazzichetto et al. 2021, Baer and Gray 2022), native plant abundance-based SDMs ((Elmendorf and Moore 2008, Boulangeat et al. 2012, Lynn et al. 2019) and even SDMs for other invasive taxa (Verhelst et al. 2016). Importantly, the direction of relationships between cheatgrass and other plant functional groups were consistent with detailed, long-term studies of plant communities invaded by cheatgrass. For example, perennial graminoids negatively affected abundance of cheatgrass (Chambers et al. 2016, Kerns and Day 2017). This suggests that existing community level studies can provide highly relevant information regarding what biotic predictors are important to include for an invasive plant abundance-based SDM, proving a priori expectations about the response of invasive plants to the biotic community.

This study also confirmed that the context in which biotic interactions occur is highly important for invasive plant abundance. The influence of biotic interactions on cheatgrass abundance was strongest when interacting with environmental suitability (Table 2.2) . This is consistent with existing research on the concept that the degree to which plant abundance is affected by competition or facilitation may depend on abiotic context (Lynn et al. 2019). Along similar lines, certain biotic interactions that influenced cheatgrass abundance probabilities only occurred above or below a certain threshold of environmental suitability (e.g. environmental suitability's interaction with shrub cover in Figure 2.1 and environmental suitability's interaction with tree cover in Figure 2.2). This implies that there may be upper or lower environmental limits for when invasive plant abundance is influenced by biotic interactions. Finally, by far the greatest influence biotic interactions had on cheatgrass abundance was found when cheatgrass abundance was already high (≥50% cover). This means, at least in this specific case study, that invasive plants may achieve levels of abundance that negatively affect its recipient communities' structure and function prior to being influenced by biotic interactions.

Implications and Future Research

This case study found that accounting for known biotic interactions with other plant species helps to explain invasive plants' abundance, with the largest improvements to the high abundance model. Given these findings, there are broader implications that can be used to improve invasive plant abundance-based SDMs. First, existing literature on the subject matter of biotic interactions provides a solid foundation to test which species provide important interactions. This is exemplified by the fact that perennial graminoids, shrubs, and trees, growth forms with known biotic interactions with cheatgrass, are all identified as in certain contexts within this study. A lack of knowledge regarding biotic interaction for invasive plant abundance is not prohibitive, further research on this subject across invasive plant species can inform what species interactions should be included alongside abundance-abased SDM environmental suitability predictions. Second, all invasive plant abundance-based SDMs can at least be marginally improved by accounting for biotic interactions, it may be particularly beneficial to include them for high abundance models. The threshold of what constitutes as "high" abundance will differ across invasive plant species, the findings of this case study suggest that inclusion of biotic interactions for SDMs capturing high abundance is recommended.

Biotic interactions can be used to improve abundance-based SDMs, the approach taken in this study is only possible because of the preponderance of cheatgrass abundance observations and co-occurring plant cover measurements . To represent biotic interactions in abundance-based SDMs for other invasive plant species lacking similarly robust datasets, alternative approaches are likely needed. If cover of plant growth forms can be used to represent important plant-to-plant interactions, remote sensing derived products that provide continuous cover values across a study region may be a fruitful alternative. Remote sensing can be used to create proxy layers representative of plant growth forms or functional traits (He et al. 2015) or can be used to create cover layers for highly generalized functional groups (i.e. tree, shrub, herbaceous) (Shi et al. 2022) that can be used directly in SDM creation as model predictors.

Finally, the focus of this case study was on competition and facilitation, other important types of biotic interactions, such as herbivory or plant-microbial interactions, were not captured in this study. Herbivory or plant-microbic interactions are identified as important types of biotic interaction for invasive plant abundance (Keane 2002, Levine et al. 2004), but are challenging to incorporate into SDMs due to a lack of data. While competition and facilitation are good starting points for representing biotic interactions, the influence the greater biotic community has on invasive plant abundance needs to be considered to fully understand how biotic interactions affect invasive plant abundance distributions. Creating data sources and methods on how best to represent these biotic interactions into SDMs is a future research area ripe for investigation.

Caveats and Considerations

Cheatgrass was selected as the species to be modeled for this case study, the ecology of this species provides some limitations on extrapolating our findings to other invasive plants. The highly generalist nature of cheatgrass (Mack 1981, Knapp 1996) means that the effects of biotic interactions on its distribution may not be as important compared to an invasive plant with stricter abiotic requirements. The highly generalist nature of cheatgrass is reinforced by the weaker predictive power of environmental suitability only models generally and that environmental suitability was a not a significant variable for low cheatgrass abundance. An invasive plant that is more environmentally constrained may have a different relationship with biotic interactions in either a positive or negative direction.

One interpretation of note on this study's results is regarding Figure 2.2, which depicts the influence of the environmental suitability and biennial forb cover on medium abundance suitability probability. The dynamic presented in Figure 2.2 shows that despite very low environmental suitability, medium cheatgrass probability is very high when biennial forb cover is also very high. In a real-world scenario where this occurs, it is highly likely that some variety of spatial factors not included in the models, such as disturbance or proximity to a road, is driving this dynamic. It is also possible that this dynamic is in part driven by the way cheatgrass abundance was categorized for this study. If the probability of medium cheatgrass abundance is decreasing as suitability increases, it is possible that what is being observed are cheatgrass populations in the process of progressing from medium to high abundance. If a cheatgrass population is growing out of the bounds of our abundance categorization, potentially driven by the same spatial phenomena that is driving high biennial forb cover, it would be observed as a decrease in probability despite an increase in environmental suitability. Figure 2.2 is called out in particular as it seems non-reflective of real-world conditions and should be interpreted with caution.

Conclusion

In this study, we asked if including biotic interactions in the form of competition and facilitation helps to predict invasive plant abundance distributions and in what contexts. We found that biotic interactions among plants used in conjunction with SDM derived environmental suitability scores improve predictions of invasive plant abundance distributions, particularly when considering how biotic variables interact with environmental suitability and when invasive plant abundance is high. As such, using biotic interactions alongside SDM outputs may be useful in certain contexts. Further research is needed regarding abundance thresholds at which biotic interactions improve prediction of habitat suitability invasive plant abundance. Exploring other methodological approaches that can represent continuous cover of biotic variables such as remote sensing derived products, and the development of data sources and methodologies regarding how best to represent non-plant to plant biotic interactions.

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CHAPTER 3 - LABELS THAT LIMIT: A FRAMEWORK FOR REDUCING SALES OF ORNAMENTAL INVASIVE PLANTS

Introduction

Invasive plants are non-native plants that are introduced, accidentally or intentionally, outside of their natural range where they are capable of persisting, growing, and spreading across that new region (Mack et al. 2000). While not all invasive plants are detrimental to their new region, certain invasive plants negatively impact ecological and economic systems. Between 1960 and 2020 the total cost of invasive plants within the US was $190 billion (Fantle-Lepczyk et al. 2022). As per Fantle-Lepczyk et al. this figure has soared over time, as the average annual cost from all invasive species increased from $2 billion in the 1960s to $21.08 billion in the 2010s. These costs are a result of economic losses, such as reduced agricultural yield, loss of water availability, and the use of resources to manage infestation (Duncan et al. 2004), as well as ecological damages, such as impairment of ecological function and biodiversity loss (Mack et al. 2000). Given these costs, approaches that reduce spread of invasive plants are likely to be beneficial to ecosystem health, invasive plant managers and policy makers, and society at large.

While non-native plants can be introduced to new regions through by a variety of means, such as for agricultural or erosion control purpose, the ornamental plant trade represents a

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common pathway of introduction for non-native plants (Lehan et al. 2013). Ornamental plants are defined as plants that are used either strictly or at least in part for aesthetic purposes. (Reichard and White 2001). The number of invasive plants that were originally introduced for ornamental purposes is disproportionally high compared to other introduction pathways. Across the US, approximately 82% of the 235 invasive woody plants were introduced for ornamental purposes (Reichard 1994). Callery pear (Pyrus calleryana) (Culley and Hardiman 2007) and Japanese barberry (Berberis thunbergii) (Silander and Klepeis 1999) are two of the examples of non-native species sold for ornamental purposes that later become highly impactful invasive plants. Even after an ornamental plant is deemed invasive, which occurs through a non-legal process which determines if the impacts from a non-native species outweigh the benefits (Invasive Species Advisory Committee 2006) and may include the use of invasiveness assessment tools (Koop et al. 2012; Roy et al. 2014; Conser et al. 2015), it is common for that species to continue to be available for purchase (Beaury, Patrick, and Bradley 2021).The continued sale of invasive ornamental plants results in a greater number of invasive plants on the landscape, which increases the probability of spread and growth of new populations, increasing the impacts and costs of these species over time (Dehnen-Schmutz and Touza 2008). Given this, there is a need to limit the sales of invasive ornamental plants.

Labeling Program Rationale

The policies surrounding the sales of invasive plants is a patchwork of federal and state regulations. At the federal level, the Plant Protection Act (7 U.S.C. §7701 et seq.) provides the US Dept. of Agriculture Animal and Plant Health Inspection Service (APHIS) with authority to regulate the importation and interstate movement of invasive plants but can only be applied to the sales of federally designated noxious plant species, which encompasses only a few invasive plant species. At the state level, the most common regulatory means of managing invasive plants is through the state's noxious weed list, but these lists are neither comprehensive (Beaury et al. 2021) nor entirely effective at preventing the sales of those species listed (Beaury, Patrick, and Bradley 2021). One study found that on average, state noxious weed lists only contained 19.6% of the species considered invasive by state or regional invasive plant working groups (Quinn et al. 2013). A separate study found that across the US, 146 regulated plant species were still available for purchase in the states in which it is specifically illegal for them to be sold (Beaury, Patrick, and Bradley 2021). While state level programs that regulate the sales of certain invasive ornamental plants exist, such as Maryland's mandatory invasive ornamental plant labeling program (COMAR 2020), or Maine's ban of selling invasive plants via 'do not plant' lists (Maine Department of Agriculture, Conservation and Forestry 2022), these programs are patchwork across the US, varying in approach, scope, and existence from state to state.

In addition to government driven solutions, the ornamental plant trade industry also plays a key role in limiting sales of ornamental invasive plants. As recently as 2020, the American Society for Horticultural Science held a workshop examining the broad topic of invasive ornamental plants (Schnelle and Gettys 2021). Despite opposition to outright bans and the long term ineffectiveness of voluntary self-bans (Hulme et al. 2018), there is evidence that members of the ornamental plant trade industry are interested in addressing this issue. One survey conducted of Maine nursery professionals found over 80% of respondents agreed that the horticultural trade played a role in the introduction of invasive plants. 98% of respondents said they would be willing to participate in a preventative measure to reduce the sale of invasive species (Burt et al. 2007). A separate industry survey found 65.3% "agreed" or "strongly agreed" that they would be willing to label invasive ornamental plants for sale (Coats, Stack, and Rumpho 2011).

Given both the patchwork regulatory environment and difficulty of the ornamental plant trade industry to implement self-bans, an alternative approach is needed. To that end, an opt-in collaborative program between industry and a certifying entity that involves labeling ornamental invasive plants may be an effective solution. This approach not only allows for retailers, governments, and/or non-profit organizations to work together to find appropriate solutions to this problem, but also brings in an additional party previously left out of this process - the consumer.

Labeling Program Evidentiary Support

Labeling programs in the agricultural industry are commonly used to better inform customers about the product they are buying and aid sellers with creating new markets for their products (Golan et al. 2001). Examples of agricultural labeling programs can be found at the federal level (e.g., Agricultural Marketing Service 2000) and state level (e.g., Colorado Department of Agriculture 2022). Non-profit organizations also use labels to certify agricultural products that comply with program standards (e.g., Rainforest Alliance 2020; Fairtrade International 2022). Labeling is also already used as a tool to prevent the spread of invasive species. The Federal Seed Act (7 U.S.C. §1551 et. seq) requires that noxious weed seed contaminants be disclosed via label when agricultural seed mixes are sold. Maryland's Department of Agriculture has their own mandatory labeling program for high-risk invasive ornamental plants (COMAR 2020).

The effectiveness of a labeling program to reduce ornamental invasive plant sales is supported by scientific literature. Half of nursery customers from urban and suburban areas preferred native or non-invasive horticultural plants to invasive ones (Yue, Hurley, and Anderson 2012). Members of the public in Portugal found that an individual's opinions on whether an invasive plant should be removed from the landscape depended upon whether they knew the plant was invasive (Cordeiro et al. 2020). When deciding whether a plant should be removed from a landscape, invasiveness was found to be more important than other factors, such as personal value or ecosystem services. This is also evidence to suggest that retailers could charge more for the sales of non-invasive plants, mitigating the costs of a labeling program. Nursery customers were willing to pay small but statistically significant premiums when offered the choice between a native, non-invasive plant versus a non-native, invasive plant (Yue, Hurley, and Anderson 2011). The willingness to pay for non-invasive plants was objectively small - invasive plants were preferred when they were discounted by $1.01-$1.66 - but it does suggest that if a non-invasive option is offered at comparable prices, customers may opt to purchase the non-invasive alternative. This price differential may also undersell opportunities for retailers, as 67% of customers were "never" or "seldom" told if the plant they were purchasing was in fact invasive (Yue, Hurley, and Anderson 2012). Collectively, this evidence suggests that disclosing a plant's invasiveness status via labeling may alter customer preference and result in customers purchasing non-invasive plants, even when sold at a small premium.

Labeling Program Benefits

Evidence suggests that a labeling program may be effective at changing customer behavior and reducing invasive ornamental sales. However, retailers may still be hesitant to adopt the program due to the uncertainties of operational costs and revenue changes. This is where collaboration between retailers and government/non-profit organizations becomes important. First, when a product is certified by a third-party organization, it results in greater program credibility (Golan et al. 2001). As such, government/non-profit participation as a certifying entity would provide more authority for interested customers when compared to selfcertification by retailers. Second, a collaborative effort would ensure that the cost of administering this program would not fall entirely upon retailers, as would happen in a voluntary code of conduct. Cost, lack of resources, and lack of personnel are all cited as barriers for industry adoption of successful preventive measures regarding the sales of invasive plants (Burt et al. 2007). The cost of a labeling program could be partially funded by the certifying agency either directly (i.e. grant funding) or indirectly (i.e. providing materials, program outreach/education efforts, etc.). By having multiple entities collaborate, costs associated with the program can be dispersed among partner organizations. Third, a labeling program stands to benefit all participating parties. Retailer program adoption may not only prevent the passage of more costly regulation but can fulfill other key company objectives. Small scale, specialty retailers can use program participation to cater to environmentally conscious customers. Large scale retailers could use program participation to better satisfy corporate sustainability pledges. Certifying partners can reduce the spread of ornamental invasive species through means that are typically not accessible to them outside of strictly regulatory means. Customers stand to benefit by increasing their knowledge of a key ecological issue and becoming an active participant in the development of a solution. By making this program collaborative, it increases program validity, avoids making retailers solely responsible for programmatic costs, and provides tangible benefits to all parties involved.

Labeling Program Framework

We conducted interviews with program representatives, industry professionals, and relevant governmental personnel, and used previously cited literature to create a programmatic framework (Figure 3.1) for an opt-in labeling program for ornamental plants. Each step in the framework is detailed below but sufficiently vague to be adapted to fit the needs of different collaborating organizations. Additionally, several existing programs can be looked to as examples of the collaborative approaches between multiple organizations that address the issues of invasive plants within the horticultural industry. Elements from each of these programs can be drawn upon and serve as models for creating a labeling pilot program:

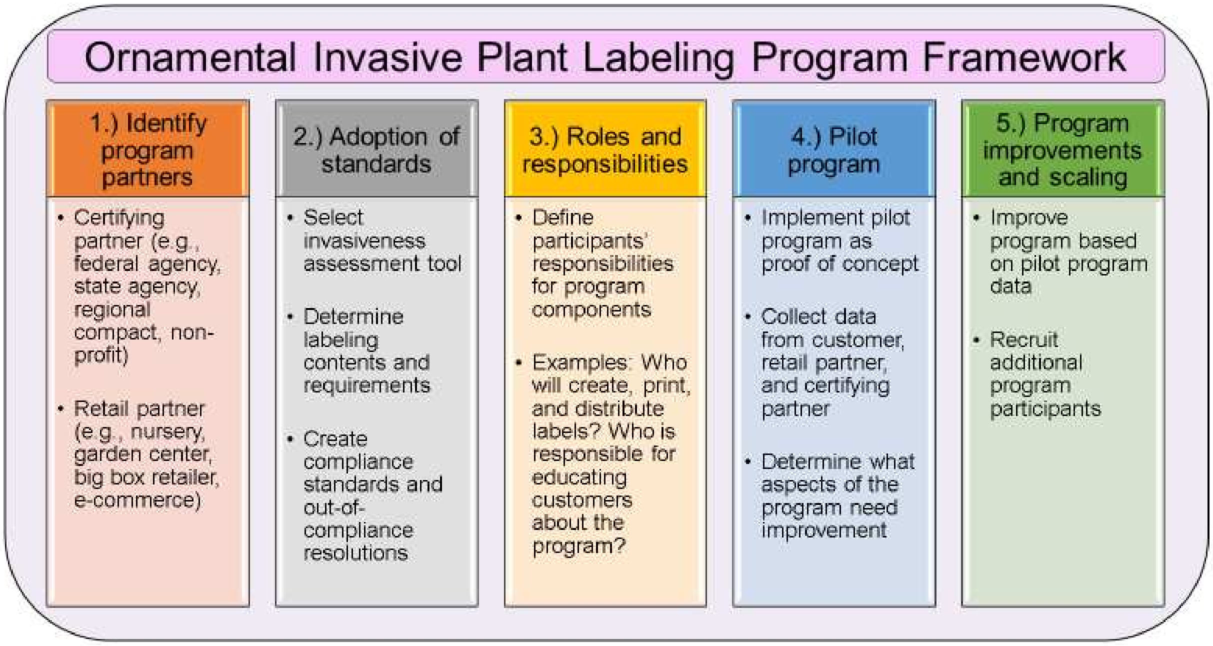

Figure 3.1: Five step framework detailing the process of creating a collaborative, opt-in invasive ornamental plant labeling program.

- The Plant Right (PlantRight 2022) program created and managed by the non-profit Land California Alliance, identifies ornamental invasive plants and educates retailers and customers about their risks, as well as provides alternative species across California. Plants are determined to be invasive based on the data driven findings of the Plant Risk Evaluator tool (Conser et al. 2015) and are assessed on a regional basis. Once invasive plants have been regionally identified, the organization builds relationships with both retailers and customers to better inform all parties about the issues associated with invasive ornamental plants and what alternatives species exist. Over the last seven years, surveys conducted by PlantRight found that listed ornamental invasive plants carried by retailers decreased from 44% to 20% (Lee 2021).

- An alternative multiorganizational approach can be found by examining the certified weed-free products program administered by the non-profit North American Invasive Species Management Association (NAISMA) (NAISMA 2018). In this approach, governmental or pseudo-governmental entities may opt into the NAISMA program. Participants receive standardized training on how to meet program standards and become certifiers for the program, capable of administering inspections and certifying participating product producers. Producers within the program area then have the choice to opt in and receive certification when their practices align with program standards. This program has expanded to 27 states and includes product inspection and certification for forage, hay, gravel, and mulch.
- The Systems Approach to Nursery Certification (SANC) program (National Plant Board 2020) serves as an excellent example how a voluntary, opt-in approach to a public-private partnership program can be created and implemented. This program is a result of government, academic, and industry representatives collaborating to create programmatic standards to reduce plant pests within the plant trade industry. Plant production facilities may opt into this program, volunteering to adhere to program standards and receiving audits by government partners to ensure program compliance.

A final note, a key distinction between the Plant Right program and this framework is that the Plant Right's program abstains from a labeling approach and instead aims for the outright removal of a plant species from a retailer's inventory. While the outright removal of an invasive plant from sale is preferable, a label-driven approach is more likely to gain industry participation.

This allows partners to continue to sell potentially profitable invasive species while also informing customers about the impacts of that purchase. The goal of this approach is to create a lower friction transition away from invasive plants, as evidence suggests a percentage of informed customers will choose non-invasive alternatives over time.

Step 1 - Identify program partners: The initial step is to identify and contact interested relevant parties. At a minimum, one retail partner and one certifying partner are required. Retailers can vary in size and may specialize in ornamental plants or be a more general retailer. E-commerce retailers should not be overlooked as potential partners, as their participation may yield large dividends given the sizable number of invasive ornamental plants available for online purchase (Beaury, Patrick, and Bradley 2021). Program participation can be extended to wholesale vendors as well. Many options exist for certifying partners, depending on the scale of the program. Partnerships with federal entities such as with the USDA's Animal and Plant Health Inspection Service or the Agricultural Marketing Service may be feasible. State partners may be found at the Department of Agriculture, Department of Natural Resources, or even academic or extension institutions. Alternatively, quasi-governmental (e.g., regional invasive plant councils), non-profits, or arboretum/botanic gardens may also serve as a credible certifying agency. Non-governmental organizations vary in terms of geographic reach, funding, and expertise, but often have greater flexibility than government entities in their ability to create and oversee programs such as this one.

Step 2 – Collaborative adoption of programmatic standards: Once parties have agreed to discuss the creation of a labeling program, a series of collaborative events such as meetings, workshops, or summits, should be held to achieve consensus among participants regarding programmatic structure and standards. Standards pertaining to label contents, compliance standards/out-of-compliance resolution, and risk assessment tools should be a key area of focus. Invasive species risk assessment tools rank a species' invasiveness using a combination of life history, species origin, climate matching and other ecological information. The use of these standardized decision-making tools ensures that the determination of a plant's invasive status is evidence-based and transparent. Several invasiveness assessment methods currently used for screening imported exotic plants to determine their invasiveness (Koop et al. 2012; Roy et al. 2014; Conser et al. 2015) can be used "out of the box", adapted by partners for regional purposes, or a new assessment method can be created whole cloth. Labels will be used to either signify plants that are non-invasive or invasive or be applied to all species sold to display their invasiveness status . Compliance standards and out of compliance resolutions are critical to agree upon prior to program execution, so all parties know how compliance issues will be handled. Compliance resolutions could range from a "stick", the loss of programmatic support from certifying entities until compliance is again achieved, to "carrot", offering additional resources to enable programmatic compliance.

Step 3 - Detail and define roles and responsibilities: In addition to developing the program's structure and standards, the roles and responsibilities of each participating organization should also be defined. The main roles of a retailer within this program may include collaborating on programmatic standards, labeling plant products, and adhering to program compliance standards. Additionally, retailers could provide education and outreach to customers about the impacts of invasive plants and alternatives that are available for purchase. The roles and responsibilities of certifying partners will include program compliance, training retailers and certifying entities on compliance standards, quality control, maintaining and administering a database of plant invasiveness assessment, and education and outreach. Continued education and outreach from certifying partners to retailers should be considered a critical component, as it has been found to increase compliance among retailers in similar programs (Oele et al. 2015). Additionally, certifying partners could also provide funding in the form of grants, if financially feasible, to retailers to improve program compliance by mitigating costs.

Step 4 - Pilot program and data collection: Once programmatic standards and organizational roles are agreed upon, a pilot program should be implemented to evaluate the program with one or a small number of retailers. During this time, partners can collect information such as customer purchasing preferences, customer knowledge of invasive plants, and programmatic costs and barriers for retailers. The goal of the survey data is to improve program performance and identify problem areas prior to scaling up the program.

Step 5 - Program improvements and program scaling: Using the information collected via surveys as well as general "lessons learned" from the pilot program, the program can be improved and scaled. Data should be continually collected to ensure program effectiveness. Collected data will also allow for the program to be evaluated and act as "proof of concept" for future partners or labeling programs. This feedback improvement mechanism will help to ensure the continued participation of all parties.

While the intention of proposing this as an adaptable framework is that many different entities at different scales could implement, ideally the scale of such a program would be regional. The rationale for a regional approach is both ecological and administrative. As invasive plants are only invasive within specific ecoregions, a regional approach would optimize the ecological benefits of such a program without overregulating species in areas in which they simply are not invasive. A regional approach would also be beneficial administratively, as a regional certifying entity composed of several states or a regional invasive species council would be able to pool greater resources and disperse program costs to help. While a state or national level program would still be immensely useful, a regional approach is ideal due to the intrinsically regional nature of the problem.

A key challenge for an opt-in labeling approach at any scale is industry adoption of the program . No business is likely to opt into a program where the costs outweigh the benefits. To address this issue, certifying entities need to ensure that the cost burden of the program is outweighed by program benefits. Initially targeting businesses that cater to customers with an environmental focus and/or have well stated sustainability goals would be ideal. Ornamental plant sellers that cater to more environmentally focused client, e.g. smaller specialty nurseries, or big box stores with stated sustainability goals that also sell ornamental plants, e.g. Walmart, would be ideal partners if an opt-in labeling program can be designed in such as way that clearly meets those businesses' needs. Additionally, certifying entities should consider the spectrum of options available to them to incentivize participation. Monetary, such as grants or tax incentives, or non-monetary, business promotion, incentives should be considered depending on the type of certifying entity that is participating.

Conclusion

While previous approaches such as industry codes of conduct (Baskin 2002), out right of bans ornamental invasive plants (Hulme et al. 2018), mandatory taxes for ornamental invasive plants (Knowler and Barbier 2005), and mandatory ornamental plant labeling programs (COMAR 2020) have been proposed, these approaches have not been successful due to industry opposition, insufficient political capital required to create such a program, and/or insufficient funding required to enforce such programs (Burt et al. 2007; Hulme et al. 2018). Given that no one regulatory program has been found to be widely successful, our proposed framework for creating an opt-in labeling program may be a valuable, alternative policy tool. The proposed opt-in labeling approach is one method that draws upon previously suggested policy solutions while bringing in retailers and customers as active participants in this process. The proposed framework is a starting point to design and adopt a pilot labeling program, while still deferring specific programmatic decisions to the collaborating organizations. While this programmatic framework is by no means a "silver bullet", it stands to leverage an underutilized means of reducing the spread and sales of invasive ornamental plants and in turn reduce their management and impact costs.

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APPENDIX: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 2 - THE IMPORTANCE OF BIOTIC INTERACTIONS FOR INVASIVE PLANT ABUNDANCE-BASED SPECIES DISTRIBUTION MODELS: A CASE STUDY USING CHEATGRASS (*BROMUS TECTORUM*).

Table S1: Data sources for cheatgrass (*Bromus tectorum*) abundance observations, number of observations per abundance categories pre spatial thinning, and citations for those data sources

Data Source	High Abund	Med Abund	Low Abund	Citation
EDDMapS	1882	3567	2853	EDDMapS. 2023. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health.
Beaury et al 2023	850	1341	3554	Beaury, E. M., C. S. Jarnevich, I. Pearse, A. E. Evans, N. Teich, P. Engelstad, J. LaRoe, and B. A. Bradley. 2023. Modeling habitat suitability across different levels of invasive plant abundance. Biological Invasions 25:3471–3483.
LANDFIRE	738	1860	8755	LANDFIRE. 2016. Remap 2016 Landfire Reference Database (LFRDB) at http://www.landfire/viewer.
SPCIS	1569	2611	4727	Petri, L., E. M. Beaury, J. Corbin, K. Peach, H. Sofaer, I. S. Pearse, R. Early, D. T. Barnett, I. Ibáñez, R. K. Peet, M. Schafale, T. R. Wentworth, J. P. Vanderhorst, D. N. Zaya, G. Spyreas, and B. A. Bradley. 2023. SPCIS: Standardized Plant Community with Introduced Status database. Ecology 104:e3947.
NISIMS BLM	1129	1293	1460	Reitsma, J. 2021. BLM – National Invasive Species Information Management System - Plants. v1.2. United States Geological Survey.
NISIMS NPS	429	69	218	Hop K, Strassman A, Sattler S, Pyne M, Teague J, White R, Ruhser J, Hlavacek E, Dieck J. 2017. National Park Service Vegetation Inventory Program Jean Lafitte National Historical Park and Preserve. Natural Resource Report. NPS/GULN/NRR—2017/1528. National Park Service, Natural Resource Stewardship and Science. Fort Collins, Colorado.

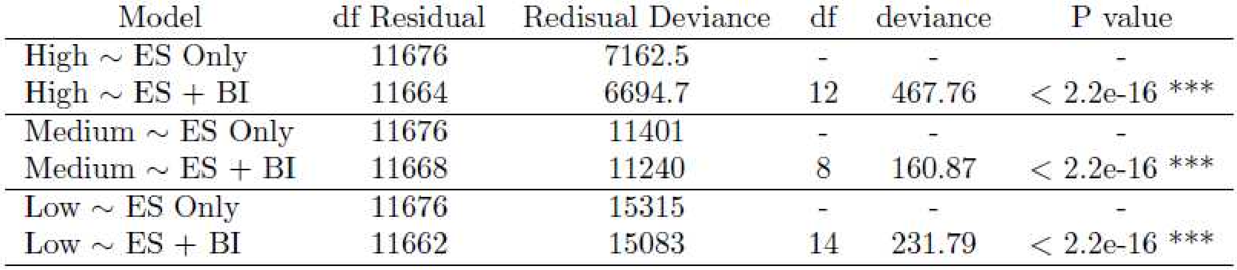
Table S2: Retained predictors for each cheatgrass abundance SDM. See Jarnevich et al. 2021 for full description of predictors and data sources

High Abundance	Med Abundance	Low Abundance
awc_mean_0_5_integer Available Water Content (Mean Depth, cm)	awc_mean_0_5_integer Available Water Content (Mean Depth, cm)	awc_mean_0_5_integer Available Water Content (Mean Depth, cm)
awc_var_0_5_integer Available Water Content (Variance in Depth, cm)	awc_var_0_5_integer Available Water Content (Variance in Depth, cm)	awc_var_0_5_integer Available Water Content (Variance in Depth, cm)
bareground.stdev_2May_integer Bare Ground Standard Deviation	bareground.stdev_2May_integer Bare Ground Standard Deviation	bareground.stdev_2May_integer Bare Ground Standard Deviation
BI_1981_2010_mean Burning Index	BI_1981_2010_mean Burning Index	BI_1981_2010_mean Burning Index
bio_02_1981_2010_800m Mean Diurnal Range	bio_02_1981_2010_800m Mean Diurnal Range	bio_02_1981_2010_800m Mean Diurnal Range
bio_03_1981_2010_800m Isothermality	bio_03_1981_2010_800m Isothermality	bio_03_1981_2010_800m Isothermality
bio_15_1981_2010_800m Precipitation Seasonality (Cv)	bio_15_1981_2010_800m Precipitation Seasonality (Cv)	bio_15_1981_2010_800m Precipitation Seasonality (Cv)
bio_17_1981_2010_800m Precipitation Of Driest Quarter	bio_17_1981_2010_800m Precipitation Of Driest Quarter	bio_17_1981_2010_800m Precipitation Of Driest Quarter
BurnFreqSum_1984to2018 Burn Frequency	bio_18_1981_2010_800m Precipitation Of Warmest Quarter	BurnFreqSum_1984to2018 Burn Frequency
caco3_mean_0_5_integer Percent Calcium Carbonate In Soil	BurnFreqSum_1984to2018 Burn Frequency	caco3_mean_0_5_integer Percent Calcium Carbonate In Soil
CHILI_90m_inhabit Continuous Heat-Load Index (CHILI)	caco3_mean_0_5_integer Percent Calcium Carbonate In Soil	CHILI_90m_inhabit Continuous Heat-Load Index (CHILI)
distance_to_water_coarse_scale_NationalAtlas Distance to Water (coarse-scale)	CHILI_90m_inhabit Continuous Heat-Load Index (CHILI)	distance_to_water_coarse_scale_NationalAtlas Distance to Water (coarse-scale)

distance_to_water_fine_scale_NHDPlus Distance to Water (fine-scale)	distance_to_water_coarse_scale_NationalAtlas Distance to Water (coarse-scale)	distance_to_water_fine_scale_NHDPlus Distance to Water (fine-scale)
ETa_Jun_Aug_2003_2021_mm_x100_int Evapotranspiration (Jun-Aug)	distance_to_water_fine_scale_NHDPlus Distance to Water (fine-scale)	ETa_Jun_Aug_2003_2021_mm_x100_int Evapotranspiration (Jun-Aug)
gHM Global Human Modification	ETa_Jun_Aug_2003_2021_mm_x100_int Evapotranspiration (Jun-Aug)	gHM Global Human Modification
mean_annual_flow_NHDplus_catchments Mean Annual Flow	gHM Global Human Modification	mean_annual_flow_NHDplus_catchments Mean Annual Flow
mTPI_270m_inhabit Multi-Scale Topographic Position Index (mTPI)	mean_annual_flow_NHDplus_catchments Mean Annual Flow	mTPI_270m_inhabit Multi-Scale Topographic Position Index (mTPI)
NDMI_median_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) median	mTPI_270m_inhabit Multi-Scale Topographic Position Index (mTPI)	NDMI_median_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) median
NDMI_sdev_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) standard deviation	NDMI_median_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) median	NDMI_sdev_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) standard deviation
PPT_March_June_1981_2018_mean Mean Spring Precipitation (Mar-June)	NDMI_sdev_Apr1_Sept30_1985_2020_90m Normalized Difference Moisture Index (NDMI) standard deviation	PPT_March_June_1981_2018_mean Mean Spring Precipitation (Mar-June)
resdt_mean_integer Depth To Restriction Layer (Mean)	PPT_March_June_1981_2018_mean Mean Spring Precipitation (Mar-June)	resdt_mean_integer Depth To Restriction Layer (Mean)
SG_k_pct_M_sl2_100m Potassium Content	resdt_mean_integer Depth To Restriction Layer (Mean)	SG_k_pct_M_sl2_100m Potassium Content
SG_n_tot_M_sl2_100m Nitrogen Content	SG_k_pct_M_sl2_100m Potassium Content	SG_n_tot_M_sl2_100m Nitrogen Content

SG_sand_M_sl2_100m Percent Sand	SG_n_tot_M_sl2_100m Nitrogen Content	SG_sand_M_sl2_100m Percent Sand
TMIN_Dec_Feb_1981_2018_mean_x100_int Minimum Temperature Winter	SG_sand_M_sl2_100m Percent Sand	TMIN_Dec_Feb_1981_2018_mean_x100_int Minimum Temperature Winter
TopoDiv_90m_inhabitx10000_Int_clip Topographic Diversity	TMIN_Dec_Feb_1981_2018_mean_x100_int Minimum Temperature Winter	TopoDiv_90m_inhabitx10000_Int_clip Topographic Diversity
water_recurrence_sum_annual_1984_2019 Water Recurrence Annual Sum	TopoDiv_90m_inhabitx10000_Int_clip Topographic Diversity	water_recurrence_sum_annual_1984_2019 Water Recurrence Annual Sum
-	water_recurrence_sum_annual_1984_2019 Water Recurrence Annual Sum	-

Table S3: Summary of ANOVA table between Environmental Suitability (ES) models only and environmental suitability plus biotic variables (ES+BI)



Model	df Residual	Redisual Deviance	df	deviance	P value
High $\sim$ ES Only	11676	7162.5	-	-	-
High $\sim$ ES + BI	11664	6694.7	12	467.76	$<$ 2.2e-16 ***
Medium $\sim$ ES Only	11676	11401	-	-	-
Medium $\sim$ ES + BI	11668	11240	8	160.87	$<$ 2.2e-16 ***
Low $\sim$ ES Only	11676	15315	-	-	-
Low $\sim$ ES + BI	11662	15083	14	231.79	$<$ 2.2e-16 ***

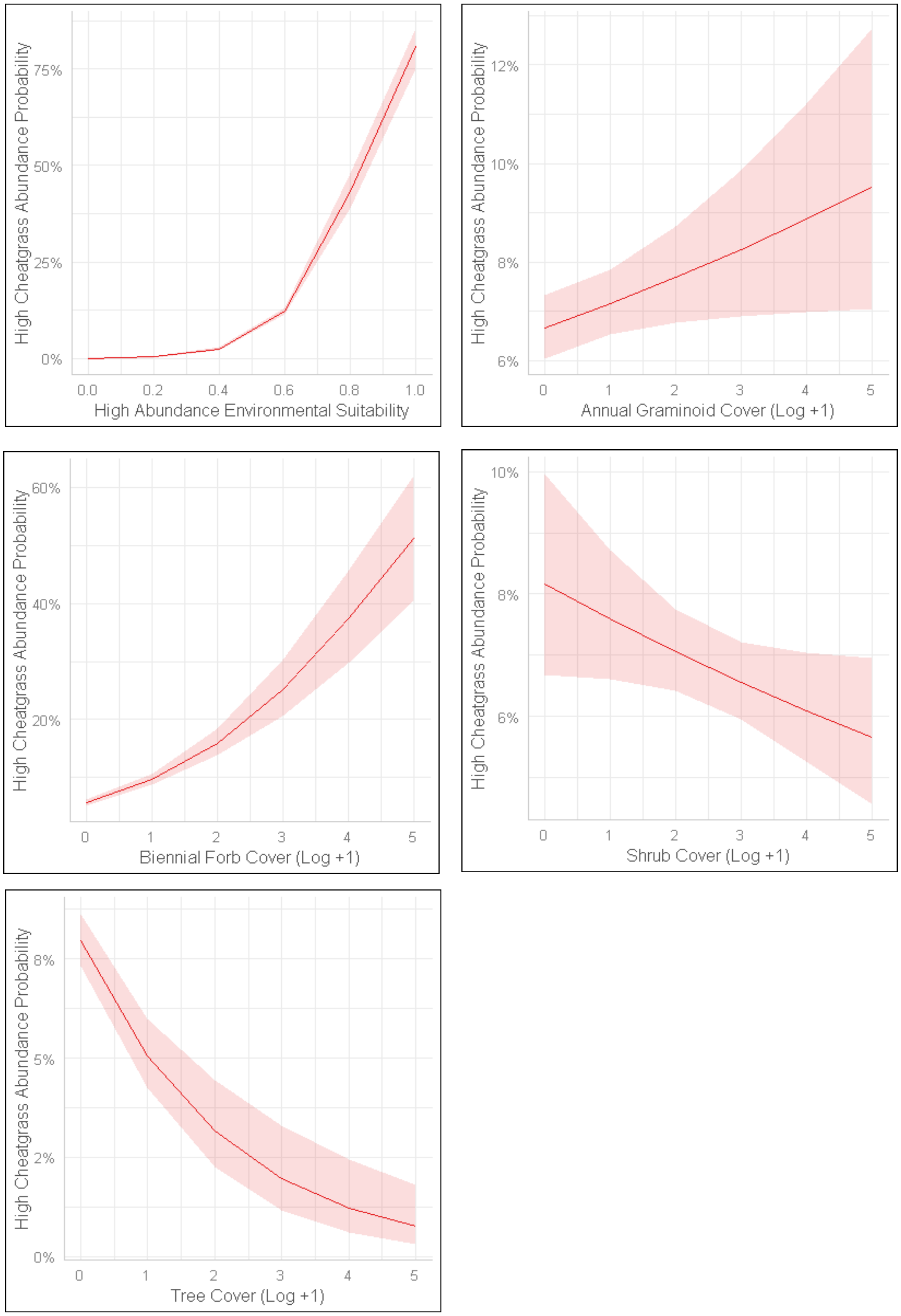


Figure S1 – Statistically significant variables for High (+50% cover) Cheatgrass Abundance Models. Y axis represents high cheatgrass abundance probability. From left to right, X axis represents Environmental Suitability, Annual Graminoid cover, Biennial Forb cover, Shrub cover, and Tree cover.

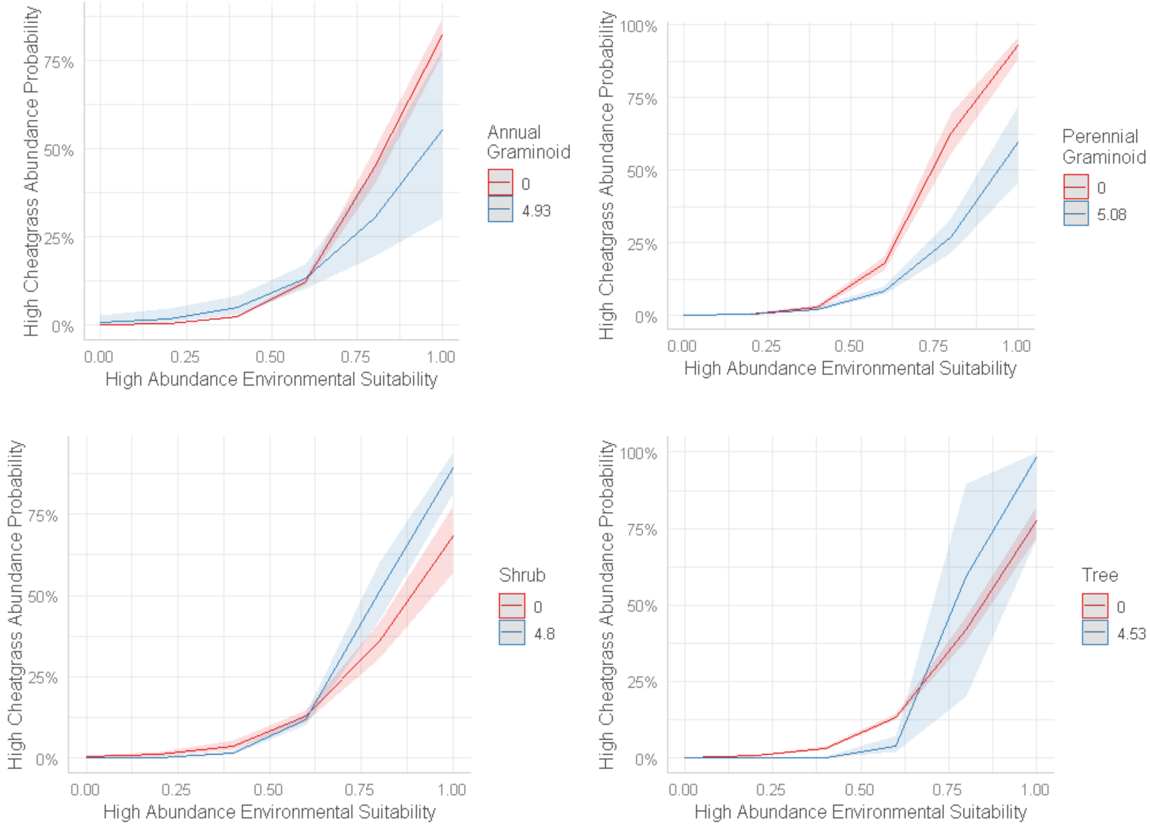


Figure S2 –The interaction of environmental suitability with biotic variable cover on high cheatgrass abundance (>50% cover) probability. Top left – Annual graminoid, minimum (0) and maximum (4.93) cover. Top Right – Perennial graminoid, minimum (0) and maximum (5.08). Bottom left – Shrub, minimum (0) and maximum (4.8) cover. Bottom Right – Tree, minimum (0) and maximum (4.53) cover.

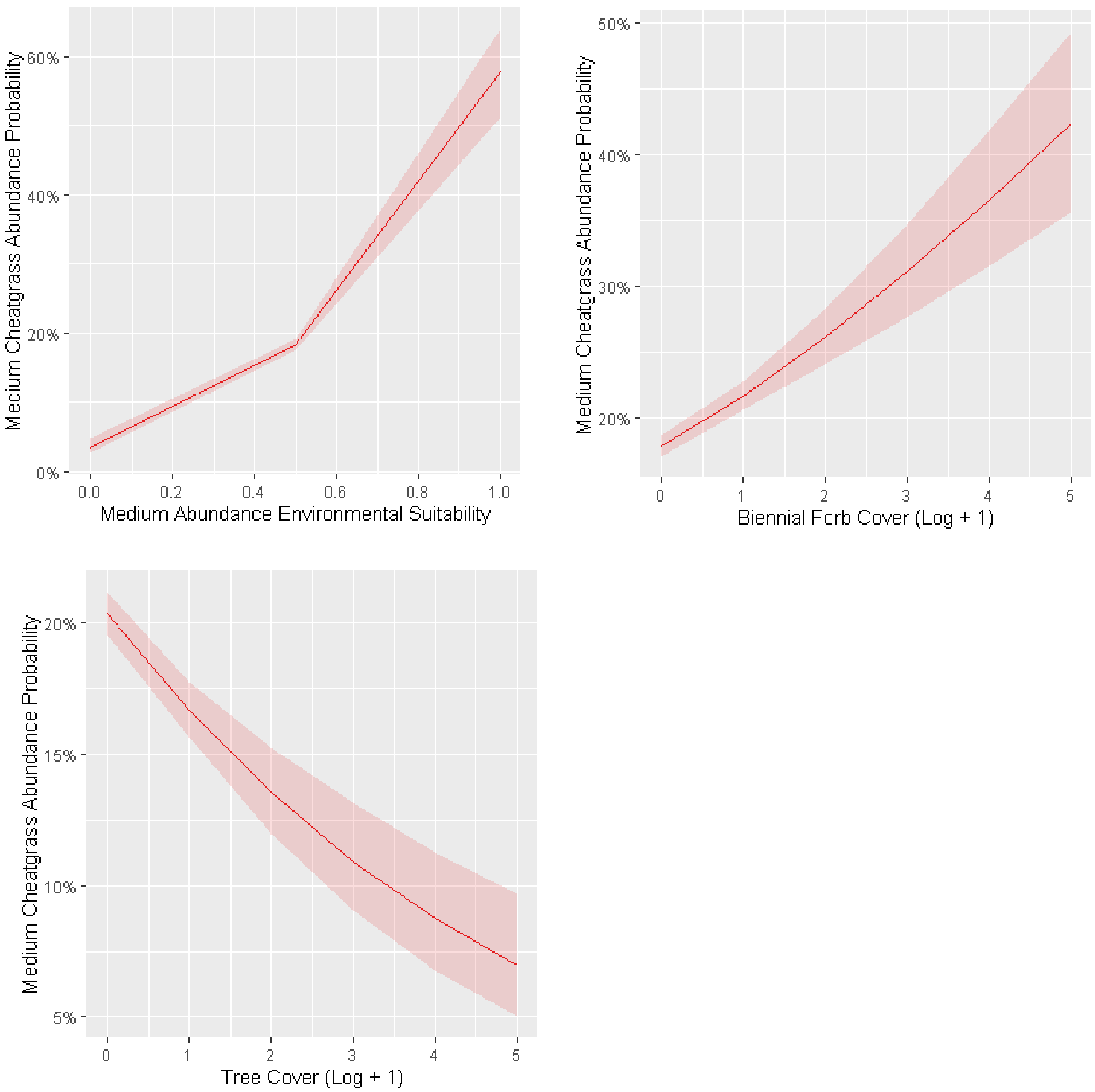


Figure S3 – Statistically significant variables for Medium (+25-50%) Cheatgrass Abundance Models. Models. Y axis represents high cheatgrass abundance probability. From left to right, X axis represents Environmental Suitability, Biennial Forb cover, and Tree cover.

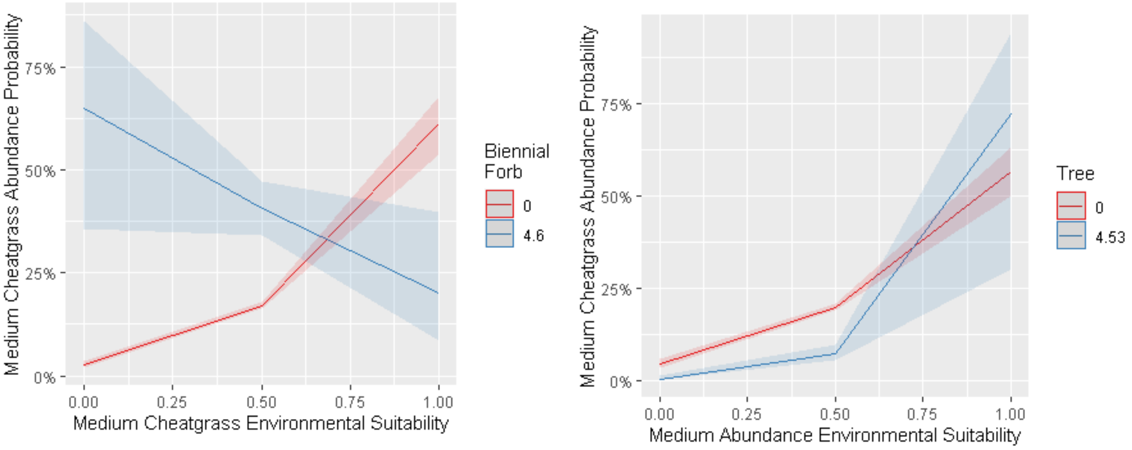


Figure S4 –The interaction of environmental suitability with biotic variable cover on medium cheatgrass abundance (+25-50% cover) probability. Left - Biennial Forb, minimum (0) and maximum (4.6) cover. Right – Tree, minimum (0) and maximum (4.53) cover.

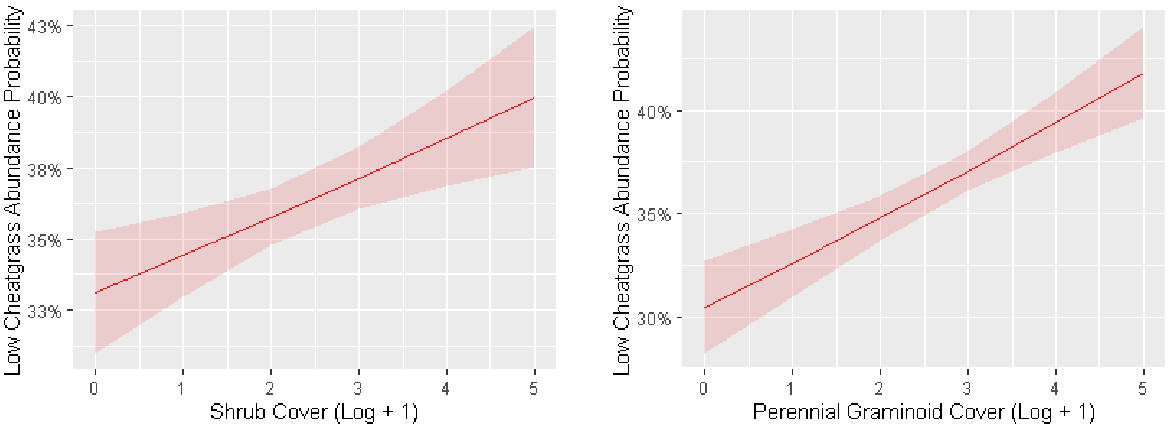


Figure S5 – Statistically significant variables for Low Cheatgrass Abundance Models. Models. Y axis represents high cheatgrass abundance probability. Left - Shrub. Right – Perennial Graminoid cover.

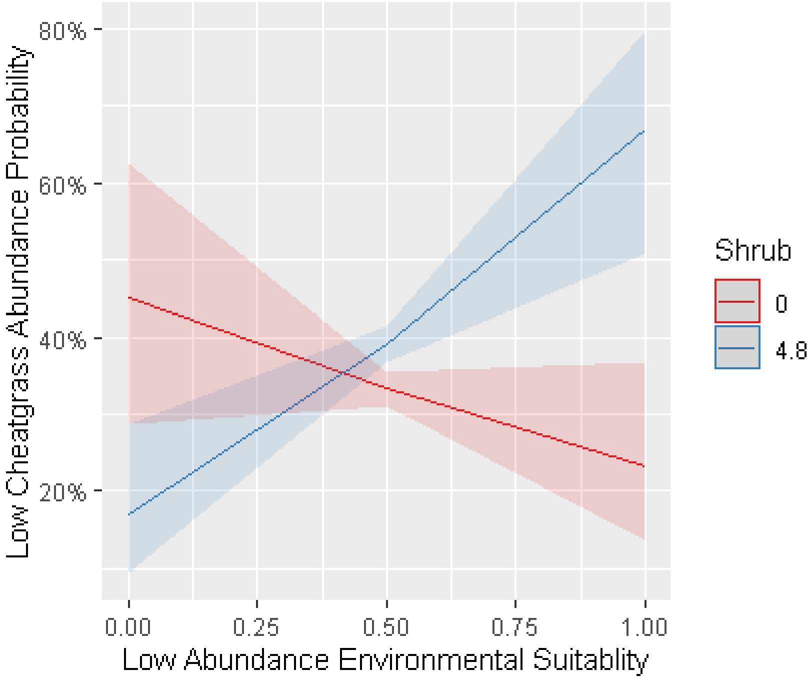


Figure S6 –The interaction of environmental suitability with biotic variable cover on low cheatgrass abundance (5-25% cover). Left - Biennial Forb, minimum (0) and maximum (4.6) cover. Right – Tree, minimum (0) and maximum (4.53) cover.