ABSTRACT

Biological invasions are a major component of global environmental change, with widespread and often unpredictable impacts on natural systems. Invasive nitrogen-fixing plants are particularly compelling in this context because they can alter the availability of a key limiting resource—nitrogen—thereby changing the conditions under which plant species interact in invaded systems. These species have the potential to reshape ecological interactions by modifying the resource environment that structures them. In this thesis, I synthesize existing literature to examine how invasive nitrogen-fixing plants influence plant communities, focusing on plant–plant interactions underlying changes in biodiversity, density, and species composition. I categorize the primary facilitative and competitive interactions that emerge following nitrogen enrichment by invasive nitrogen-fixing species, and then extend this approach by considering how these interactions co-occur within invaded communities. Across studies, the balance of facilitation and competition often shifts depending on environmental context, invader abundance, recipient community composition, and stage of invasion. I further explore how these invasion-associated interactions intersect with successional processes, highlighting potential avenues for how the effects of invasive nitrogen-fixers may change as communities develop over time. Overall, this synthesis shows that community-level impacts of invasive nitrogen-fixing plants are best understood as the outcome of multiple, interacting processes.

NITROGEN-FIXING PLANTS AND INVASIONS: A MECHANISTIC APPROACH TO COMMUNITY IMPACTS

By

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INTRODUCTION

Biological invasions have become a significant component of global environmental change (Vitousek et al. 1997; Pyšek and Richardson 2010). Human activities have resulted in the transport of species outside of their native range at unprecedented rates, resulting in an increasing number of established non-native species worldwide (Vitousek et al. 1997). As the number of species introduced to new geographic ranges increases, the frequency, extent, and intensity of the ecological impacts associated with those species also increases (Vitousek et al. 1990; Pyšek and Richardson 2010).

The impacts of invasive species are incredibly wide-ranging and can affect multiple levels of biological organization. Invasions can cause declines in native biodiversity, shifts in community composition, and changes in species dominance (Parker et al. 1999). At the same time, invasive species can alter ecosystem processes, including nutrient cycling and disturbance regimes (Vitousek et al. 1990; Pyšek and Richardson 2010). In some cases, these changes are significant enough to fundamentally restructure ecosystems (Vitousek and Walker 1989).

Importantly, these impacts are not uniform. The effects of a given invasive species can vary across spatial and temporal scales, and depend on the environmental context in which the invasion occurs (Strayer et al. 2006). The same species may have relatively small effects in one system, while driving substantial ecological change in another (Van Riper and Larson 2009; Ortiz and

Wolf 2024). Even within a single system, impacts can shift over time as the invasion progresses or as environmental conditions change (Strayer et al. 2006). This variability makes it difficult to generalize about invasion impacts or compare results across studies (Parker et al. 1999).

As a result, understanding and predicting the impacts of invasive species is a significant challenge. While many studies have focused on documenting the magnitude and direction of invasion impacts, this catalog only really captures what is happening, not how those impacts arise (Levine et al. 2003). Similar observed outcomes can be generated by very different underlying processes, and without understanding those processes, it is difficult to explain variation in impacts or predict when they will occur (Parker et al. 1999).

In this review, I use invasive nitrogen-fixing plants (hereafter N-fixing plants) as a system for examining the processes underlying invasion impacts. N-fixing plants are disproportionately represented in global catalogues of invasive species (Daehler 1998). These species share a common and well-defined mechanism of impact—the ability to fix atmospheric nitrogen—which provides a consistent starting point for comparison across systems (Scherer-Lorenzen et al. 2007). By increasing the availability of a key limiting resource, N-fixing plants can fundamentally alter the resource environment within invaded communities (Vitousek and Walker 1989). This shift in resource availability has important consequences for plant–plant interactions, changing the balance of facilitation and

competition and, in turn, influencing patterns of community structure and diversity (Callaway and Walker 1979; Ortiz and Wolf 2024).

Here, I focus specifically on the processes underlying community-level impacts of invasive N-fixing plants. I take a mechanistic approach, examining how these species generate novel plant–plant interactions within invaded communities, and how those interactions contribute to changes in community structure and diversity. To do this, I synthesize findings from studies examining community-level impacts of invasive N-fixing plants. Because this body of literature is relatively limited and uneven across systems, this review is necessarily qualitative and intended as a first step toward identifying general patterns and mechanisms that can guide future research.

1. Definitions

Before proceeding, I define a set of key terms used throughout this review. Because terminology in invasion ecology is not always applied consistently, clarifying these definitions helps ensure comparability across studies and clarity in interpretation. Additionally, many of these terms play a different role in everyday language than their very specific meanings in ecology. Clarifying their meaning in the context of this review should allow a broad range of readers to avoid confusion.

Abiotic: The non-living physical and chemical components of an ecosystem, including soil characteristics, climate, and salinity (Marchetti et al. 2023).

Abiotic stress: Non-living environmental factors that negatively impact survival or reproduction of living organisms in an ecosystem. Some examples of abiotic stressors include drought, extreme temperatures, and nutrient deficiencies (Marchetti et al. 2023).

Allelopathy: A form of plant interference where one plant affects the growth, survival, or reproduction of another through the release of chemical inhibitors (Hierro and Callaway 2021).

Biotic: The living components of an ecosystem, including plants, animals, and microorganisms (Marchetti et al. 2023).

Community-level impacts of invasive species: A measurable change in the properties of invaded plant communities. These impacts are typically measured in changes in species and functional richness, diversity, and composition (Ricciardi et al. 2013; Jeschke et al. 2014).

Condition: Environmental factors that affect an organism's performance but cannot be depleted. Examples include temperature, salinity, and pH (Marchetti et al. 2023).

Exploitative competition: Interactions between two or more individuals or species, where both are negatively affected (−,−). Occurs when species share a limiting resource. The limiting resource mediating competition must be essential

for survival and reproduction in some way, and for plants is most often light, water, or nutrients (Marchetti et al. 2023).

Facilitation: Interactions between two or more organisms, where at least one species benefits and the others are either positively (+,+) or neutrally affected (+,0) (Bertness and Callaway 1994; Stachowicz 2001; Marchetti et al. 2023). Facilitation can be either a direct interaction, where one species facilitates others by modifying physical or biotic conditions, or an indirect interaction, where one species indirectly reduces consumption of or competitive pressure on another (Bertness and Callaway 1994; Bulleri et al. 2008).

Indirect effects: The overall effect of one species on another species, mediated by a shared resource or a third species with which both actors interact (Marchetti et al. 2023).

Inferior competitor: A species that is less efficient at uptake or use of a resource in limited supply, compared to a superior competitor, often leading to a decline in the species' population (Marchetti et al. 2023).

Invasions: A term encapsulating the process by which non-native species invade natural systems. Typically understood as a process that occurs over time, with non-native species progressing through four stages—transport, colonization, establishment, and spread or impact—before reaching the status of invader (Richardson et al. 2000; Lockwood et al. 2013; Blackburn et al. 2011).

Invasive species: Non-native species that have spread from a point of introduction and have some demonstrable ecological or economic impact. (Davis et al. 2000; Young and Larson 2011).

Invasibility: Describes the susceptibility of a community or habitat to the establishment and spread of non-native/invasive species (Alpert et al. 2000).

Invasiveness: Describes the traits that enable a species to invade a new community or habitat (Alpert et al. 2000).

Native species: Species existing in the geographic range in which they evolved (Pyšek et al. 2004; Blackburn et al. 2011).

Nitrogen-fixing plants: Broad group of plants with a symbiotic association with nitrogen-fixing bacteria, capable of converting atmospheric nitrogen into reactive, biologically usable nitrogen. Legumes have a symbiotic relationship with Proteobacteria (e.g. *Bradyrhizobium* spp. and *Rhizobium* spp), while actinorhizal N-fixers have a symbiosis with actinomycete bacteria (Weil and Brady 2017; Hughes et al. 2025). N-fixing plants will be covered further in the section below.

Nitrogen cycling: Biogeochemical process through which nitrogen moves between the atmosphere, soil, water, and living organisms. Nitrogen cycling can be understood broadly in terms of pools and fluxes. Pools refer to stored nitrogen in ecosystem compartments— atmosphere, soils, or organisms—while fluxes are the transfers between pools (Ehrenfeld 2003; Castro-Díez et al. 2014).

Nitrophilous: Term for broad category of fast-growing plant species that thrive in soil with high nitrogen content (Moreau et al. 2014).

Non-native species: Species that have been introduced outside of their native geographic range via human action (Pyšek et al. 2004; Blackburn et al. 2011). Sometimes referred to as “exotic” or “alien” species in the literature.

N-sparing: Occurs when the N-fixing plant’s reliance on atmospheric nitrogen reduces their uptake of soil nitrogen, leaving more soil nitrogen available for other species (Scherer-Lorenzen et al. 2007).

Plant communities: A group of interacting plant species in the same location (Marchetti et al. 2023).

Resource: Environmental factors that affect an organism’s performance and that can be depleted (unlike conditions); individuals may compete for resources. Examples of resources include soil nutrients, water, and space (Marchetti et al. 2023).

Superior competitor: A species that uses more or all of a resource in limited supply, lowering the availability of the resource for other species and eventually driving the other species extinct (Marchetti et al. 2023).

Symbiosis: A close, prolonged association between two or more different biological organisms (Hughes et al. 2025).

2. Background information on N-fixing plants

With these definitions in place, I now turn to the focal group of this review: N-fixing plants. Understanding the biology and ecological function of

these species is essential for interpreting their impacts on invaded systems, particularly their role in altering nitrogen cycling.

The term N-fixing plants refers to the broad category of plants with the ability to convert atmospheric nitrogen into reactive forms; these species are responsible for generating a large portion of the nitrogen available to biological organisms (Osman 2013; Weil and Brady 2017). This process is carried out by symbiotic bacteria, primarily genera collectively referred to as Rhizobia, which associate with plant species in the Fabaceae family, commonly called legumes (Hughes et al. 2025). These bacteria live in root nodules and convert nitrogen gas (N_2) into ammonia (NH_3), which can be used by the plant in exchange for carbohydrates. While legumes make up the majority of N-fixing plants, some non-leguminous species form similar symbioses with actinomycete bacteria, and are referred to as actinorhizal plants (Osman 2013; Weil and Brady 2017).

Because nitrogen fixation is mediated by microbial symbionts, its occurrence depends on both the presence of compatible bacteria and resource availability (Osman 2013; Weil and Brady 2017; Hughes et al. 2025). N-fixing bacteria may not always be present in the soil, particularly when the host plants expand beyond their native range into systems lacking other N-fixers (Wielbo 2012; Pierre et al. 2017). Additionally, fixation rates are strongly influenced by soil nitrogen availability. Nitrogen fixation is an energy-intensive process, and both plants and microbes will preferentially use available soil nitrogen when it is

abundant, only shifting to atmospheric fixation under nitrogen-limited conditions (Smercina et al. 2016; Zheng et al. 2019).

Through this symbiosis, N-fixing plants (leguminous or actinorhizal) are able to access a relatively independent source of nitrogen. Fixed nitrogen is incorporated into plant tissues as organic compounds, including proteins and other essential molecules (Osman 2013; Weil and Brady 2017). Because this nitrogen is stored in organic form, it is not immediately available to other plants in the system (Osman 2013; Weil and Brady 2017).

Access to this additional nitrogen allows N-fixing plants to adopt growth strategies more typical of plants in high-nitrogen environments, including high photosynthetic rates, relatively rapid growth, and often greater productivity than non-N-fixing species (Scherer-Lorenzen et al. 2007; Hughes et al. 2025). This capacity can confer a strong advantage to the plants in nutrient-poor environments. N-fixing plants are able to establish and persist in systems where nitrogen limits the growth of other species, while maintaining growth strategies associated with high nitrogen availability (Funk and Vitousek 2007).

Although each N-fixing plant is the initial beneficiary of the nitrogen fixed by its symbionts, this nitrogen can become available to other plants through several pathways. Most commonly, nitrogen enters the soil through the decomposition of nitrogen-rich plant tissues, such as leaf litter or whole plants during senescence (Maron and Connors 1996; Ehrenfeld 2005; Dornbusch et al. 2018). Because this tissue often has a relatively low carbon to nitrogen ratio (C:N

ratio), it decomposes quickly, contributing to increases in soil nitrogen availability (Ehrenfeld 2005). N-fixing plants may also increase soil nitrogen indirectly through "N-sparing," where their reliance on atmospheric nitrogen reduces their uptake of soil nitrogen, leaving more available for other species (Scherer-Lorenzen et al. 2007; von Felton et al. 2009; Ortiz and Wolf 2024). In some cases, fixed nitrogen may also be transferred directly to neighboring plants through mycorrhizal networks. That said, the latter two pathways contribute relatively little compared to decomposition (Watt et al. 2003; Scherer-Lorenzen et al. 2007).

As a result of these processes, N-fixing plants are often associated with changes in nitrogen cycling at the ecosystem level (Ehrenfeld 2003; Castro-Díez et al. 2014). These effects are particularly pronounced when N-fixers invade systems that lack a native nitrogen-fixing species, where they introduce a novel functional role. In these contexts, invasive N-fixers can substantially increase soil nitrogen availability, either by enlarging nitrogen pools or by accelerating fluxes between the atmosphere, soil, and plant biomass (Ehrenfeld 2003; Castro-Díez et al. 2014). Because fixation is most active under nitrogen limitation, these effects tend to be strongest in nutrient-poor environments (Smercina et al. 2016; Zheng et al. 2019).

Changes in nitrogen availability have important consequences for other plant species. Nitrogen is an essential macronutrient involved in the synthesis of proteins, nucleic acids, and other compounds, and plays a central role in plant

growth and physiology (Novoa and Loomis 1981; Ohyama 2010). Increased nitrogen availability can lead to higher growth rates, greater leaf area, and increased photosynthetic capacity, while nitrogen limitation can constrain these processes (Ohyama 2010).

While nitrogen is essential for all plants, the uptake and use of nitrogen can differ across plant species (Chapin et al. 1986; Tilman 1987; Xu et al. 2012). These differences are shaped by physiological traits, life history strategies, and adaptations to nutrient availability (Hughes et al. 2025). Some species, often referred to as nitrophilous, are particularly efficient at taking up and utilizing nitrogen and tend to grow rapidly under high-nitrogen conditions (Grime and Hunt 1975; Moreau et al. 2014). Others are adapted to low-nutrient environments and may respond less strongly to increases in nitrogen. Differences in nitrogen allocation—for example, to leaves versus roots—can also influence how species respond to nitrogen enrichment and compete with one another (Tilman 1987; Congreves et al. 2021).

Although the mechanisms underlying nitrogen uptake and use are complex, the key point for this review is that species differ in their responses to increased nitrogen availability. As a result, nitrogen enrichment by N-fixing plants has the potential to alter interaction dynamics within plant communities, favoring some species over others and ultimately contributing to shifts in community composition.

3. Plant–plant interactions as mechanisms of community change

Ecosystem-level nitrogen enrichment represents one way in which invasive N-fixing species impact the systems they invade (Ehrenfeld 2003). However, ecosystems are inherently interconnected, and changes at one level of biological organization often have impacts at others (Lockwood et al. 2013). While ecologists frequently distinguish among genetic, population, community, and ecosystem-level impacts of invasive species, these categories are not independent in practice (Lockwood et al. 2013). Changes in nutrient cycling associated with invasive N-fixers can cascade across levels of organization, influencing community dynamics through shifts in resource availability (Ortiz and Wolf 2024). Because nitrogen is a key limiting resource in many terrestrial systems, its enrichment can fundamentally alter the resource environment experienced by plants, the interactions between plants, and ultimately the interactions among the consumers of plants and their predators (Vitousek and Howarth 1991; Marchetti et al. 2023; Ortiz and Wolf 2024).

Community composition and diversity are often maintained and altered by interactions among species (Bruno et al. 2003; Brooker 2006). This suggests that understanding the community-level impacts of invasive N-fixing plants requires a mechanistic perspective focused on resulting plant–plant interactions, specifically on how invasive N-fixers shift the balance between competition and facilitation. Framing the question in this way provides a way of linking relatively well-understood ecosystem-level changes to the more variable and

context-dependent impacts at the community level, and forms the foundation for the approach of this review.

3.1 Competition

Competitive interactions play a central role in structuring plant communities, particularly when the competitive effects are not equally negative for the involved species (Marchetti et al. 2023). Competition can act as a biotic filter, determining which species persist in the community (HillRisLambers et al. 2012).

The competitive ability of a given species is related to both its efficiency in consuming a limited resource and its ability to survive at a lower resource threshold relative to its competitors (Tilman 1977). Those that are better at accessing a resource are typically the superior competitor, and can competitively exclude or even drive competitor species to extinction. In general, the effect of a competitive interaction is stronger between species when they have a higher resource use overlap (Marchetti et al. 2023). However, the strength and outcome of competitive interactions are highly context-dependent and may shift in response to environmental conditions or changes in resource supply (Chamberlain et al. 2014).

3.2 Facilitation

Facilitative interactions between plants are also a driving force in structuring ecological communities (Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003). At a very broad level, facilitation by one plant generally results in a positive effect on the growth, survival, and reproduction of existing plant species in the community or the establishment of new species (Callaway 2007). Facilitation can also be understood as a reduction in competition, as facilitators can increase the presence or access to a limiting resource, reducing competition over that particular resource (Callaway and Walker 1997). Thus, facilitation in plant communities is often associated with an increase in species diversity, biomass, or a change in the community composition (Callaway 2007; McIntire and Fajardo 2013; Cavieres et al. 2021).

One of the primary ways facilitation influences community dynamics is through the amelioration of abiotic stress. Facilitating species may reduce these stressors through habitat modification, often by altering microclimatic conditions or resource availability, ultimately creating more favorable conditions for both themselves and neighboring plants (Brooker et al. 2008; Soliveres et al. 2011).

Facilitation is also closely tied to the concept of the niche in ecological communities (Bruno et al. 2002; Callaway 2007). When a facilitator modifies the environment, through any given mechanism, they can increase the presence of or access to a resource. This means that plants in the surrounding area can utilize resources that they previously did not have access to. Facilitation allows a species to utilize a larger portion of available resources, which in the context of the niche,

essentially means the plant is using more of the fundamental niche than if it was growing without the facilitator (Bruno et al. 2002; Schöb et al. 2012). In some cases, these modifications may be significant enough to create novel niches, enabling the establishment of species that would not otherwise exist in the system (Hughes and Denslow 2005; McIntire and Fajardo 2014). This process of niche expansion or construction highlights the potential for facilitation to drive shifts in community composition through the addition of new species or functional groups (Hughes and Denslow 2005; Vetter et al. 2018).

4. Objective of the review

The objective of this review is a qualitative examination of the processes underlying community-level impacts by invasive N-fixing species. I aim to examine the types of novel plant–plant interactions that are introduced following invasion, and often resource alteration, by N-fixing species. These facilitative and competitive interactions, which I refer to as pathways of community change, represent the mechanisms by which non-native N-fixing species restructure community dynamics in the systems they invade. The pathways incorporate information about the mechanism by which the invasive species interacted with the resident species and the identity of the species involved in the interaction. I will not offer a general review of community impacts by invasive N-fixing species, as my qualitative synthesis does not provide enough information to make

those generalizations. Rather, the focus of this review will be on the common types of facilitative and competitive interactions documented by researchers exploring the impacts of invasive N-fixing species on measures of community change, including species biodiversity, density, and community composition.

From there, I consider how these interactions co-occur and shift in importance within plant communities. Facilitation and competition are almost never operating in isolation, and the balance between them can change depending on environmental context, species traits, and where a system is in the invasion process. Thinking about impacts in this way also provides a way to approach the temporal dynamics of invasion, particularly how the relative importance of different interactions, and therefore their outcomes, may change over time.

Ultimately, I will use this review to approach the following questions: (i) How does resource alteration by N-fixing species introduce novel interactions in invaded communities? (ii) What plant–plant interactions underlie impacts on species diversity, density, and community composition? (iii) What ecological factors influence which interactions dominate in a given system? and (iv) How can a mechanistic perspective help explain how invasion impacts change over time?

METHODS

1. Literature search methods

I searched the Web of Science database for literature within the years 1970–2025 using queries I developed based on the aim of the review. I refined the search queries in order to produce higher quantities of relevant results. The search queries that produced the papers used in this review are listed below:

Invasion ecology background literature (non-experimental)

1. Plant invasion ecology (All Fields)
    a. Sort by citations: highest first
2. Community invasibility (All Fields)
    a. Sort by citations: highest first
3. Invasive species impacts (All Fields)
    a. Sort by citations: highest first
4. Invasive species facilitation (All Fields)
    a. Sort by citations: highest first
5. Invasive species competition (All Fields)
    a. Sort by citations: highest first
6. Plant invasion (All Fields) and ecosystem process* (All Fields)
    a. Sort by citations: highest first
7. Invasional meltdown (All Fields)
    a. Sort by citations: highest first
8. Nitrogen fixation (All Fields) and invasion (All Fields)
    a. Sort by citations: highest first

Experimental literature

1. Fabaceae (All Fields) and facilitation (All Fields)
2. legum* (All Fields) and facilitation (All Fields) and invasiv* (All Fields)
3. actinorhizal plant (All Fields) and facilitation (All Fields) and invasiv* (All Fields)
4. nitrogen fixation (All Fields) and facilitation (All Fields)
5. legum* (All Fields) and invasional meltdown (All Fields)

6. invasiv* legum* (All Fields) and community impacts (All Fields)
7. invasiv* legum* (All Fields) and compet* (All Fields)
8. invasiv* legum* (All Fields) and species richness (All Fields)
9. invasiv* legum* (All Fields) and biodiversity (All Fields)
10. legum* impacts (All Fields) and invasion ecology (All Fields)
11. actinorhizal plant (All Fields) and invasion ecology (All Fields)
12. legum* (All Fields) and shannon diversity (All Fields) not agricultur* (All Fields)
13. invasiv* legum* (Topic) and biomass (All Fields)

A total of 1,747 experimental papers were produced by the above search queries (under the experimental literature category) and were screened via title and abstract to determine if the study was experimental and focused specifically on invasive N-fixing plants. This screening involved some outside research to determine if the focal species was considered non-native or invasive in the studied region. This process produced an initial pool of 116 papers, including some additional papers found through forward and backward literature searches.

I then systematically read through the 116 experimental papers and included the papers that fit the following criteria for inclusion:

1.1 N-fixer classified as non-native or invasive

I included papers with focal species that were either classified as non-native or invasive. The focus of this review is on introduced N-fixing plants with significant ecological impacts, which are typically classified as invasive. However, there are certain barriers to classifying a species as invasive, including lack of research on impacts and differing definitions of the term invasive

(Richardson et al. 2000; Valéry et al. 2008). Thus, I am including both invasive and non-native N-fixing species to account for all possible impacts, even those by N-fixing species that have not yet been classified as invasive.

1.2 Plant-plant interactions

This criterion specified that the interactions covered in the experimental papers must include those between the invasive N-fixer and other plant species. This criterion excluded papers covering interactions between an N-fixer and a pollinator, herbivore, or microbe.

1.3 Paper reports measurable impact on plant community biodiversity, density, or composition

This criterion ensured that the papers included in the sample addressed the community-level impacts of invasive N-fixing plants. Papers excluded from this category included those that focused only on the impact of an invasive N-fixing plant on nutrient cycling or microbial communities, as well as those that covered the invasiveness of an N-fixing species without identifying community impacts.

1.4 N-fixer is a clear driver of the impact

This criterion ensured that the papers included in the sample distinguished the impact of the invasive N-fixing species on the community from other factors. This does not necessarily mean that no other conditions or species were involved

in the impact, only that the impact of the N-fixer was isolated enough to make claims about interactions specific to N-fixing species.

1.5 Non-agricultural and non-urban focus

This criterion excluded experimental papers exploring the role of invasive/non-native N-fixing plants in agricultural and urban settings. Literature with an agricultural focus often includes manipulation of the environment by researchers with the goal of maximizing productivity of the environment for humans. Focusing on the role of an invasive N-fixer in maximizing agricultural productivity does not provide as much insight into how it may affect growth and community composition in a more naturally occurring environment. Similarly, studies conducted in urban settings do not replicate natural systems to the degree necessary to make insights about the role of invasive N-fixing species in plant communities.

The literature search produced 45 individual papers that met the five criteria. In cases where the same researcher conducted a large quantity of studies in the same system on the same invasive N-fixing species, I included only the most relevant or highly cited paper in my sample, so as not to skew my results towards the findings of that particular researcher. This approach was only applied to papers by Peter Vitousek (see Vitousek and Walker 1989).

2. Qualitative paper data collection

Qualitative data were collected on the 45 papers in the sample. The categories for data collection, response options, and the approach to finding information for each category are listed below:

Table 1: Qualitative information collected from 45 examined papers. Includes categories for data collection, response options, and the approach to finding information for each category.

Data point	Options	Approach
N-fixer genus and species	-	As stated in the paper.
Type of N-fixer	Legume, Actinorhizal	As stated in the paper.
N-fixer growth habit	Woody, Non-woody	As stated in the paper.
Invasive status	Invasive, non-native	If a species was described as invasive or non-native in the paper, then that was used for the data point. If other language was used, I first used the context of the paper to make a determination. If context did not provide enough information, I searched regional invasive species and noxious weed lists, as well as other literature on the same species in the same environment, for a classification. If there was no indication of the species being considered invasive, I classified it as non-native.
Study system	-	As stated in the paper. North American prairies were classified as grasslands (Carpenter 1940).
Is the study system low-nutrient?	Yes, No, N/A (greenhouse), Not reported	As stated in the paper. If not stated in the paper, I checked for other papers in the same system to see whether they indicated that the

		environment was or was not low-nutrient.
Location of study	Latitude and longitude	As stated in the paper. If latitude and longitude were not reported, the values were estimated using the study site name and Google Maps.
Duration of data collection	0–1 years, 1–3 years, > 3 years	Information on timing of data collection was found in the methods section. Papers were divided into three categories: 0 < years ≤ 1, 1 < years ≤ 3, years > 3.
Type of study	Experimental, Observational	Experimental studies were often conducted in greenhouses, or involved manipulations of conditions in the field. Observational studies involved collection of data without manipulation.
Measure of biodiversity	-	The metric used to measure changes in community biodiversity in the study (ie, species richness, Shannon-Wiener Biodiversity Index). Some studies included multiple metrics.
Measure of density	-	The metric used to measure changes in community density in the study (ie, biomass, percent cover). Some studies included multiple metrics.

In order to collect information on the distribution of study systems and study species, I ended up inflating the sample size somewhat to account for studies that were conducted in multiple distinct systems or examined multiple invasive N-fixing species. If one paper discussed studies in multiple systems, I counted each of those systems as separate results or as a separate count towards a

pathway. This resulted in 48 different study systems. As mentioned above, I did not do analyses on these characteristics, but this method of counting means that my final number of studies was greater than the 45 papers.

3. Categorizing pathways of impact

Creation of the pathways of impact in this review was initially guided by a prior literature review conducted in the Fall of 2024. The previous review centered around categorizing types of facilitative interactions between legumes—native or invasive—and non-native species. The initial categories of facilitative interactions were refined based on examination of the literature on invasive N-fixing species.

The grouping of papers was largely qualitative. Papers were initially separated based on whether the authors indicated facilitation or competition as driving the impact. The papers were then analyzed again for patterns in the types of facilitative and competitive interactions occurring between N-fixers and surrounding plant species. Given the relatively small number of papers, I determined that three or more papers with a similar type of interaction could constitute a pathway.

Many papers did not fit cleanly into just one pathway. Therefore, I sometimes included the same paper in multiple categories. 9 papers of the 45 were included in more than one category.

4. Organization of the paper

The results section of this review lays out the characteristics of the examined papers using the qualitative information collected, including study species, geographic location, biome, and study methods. It also briefly outlines the different categories of facilitative and competitive interactions (pathways) along with the associated literature.

The discussion includes four sections. The first two sections outline the facilitation and competition pathways in greater detail, including examples from the literature. The third examines how facilitative and competitive pathways co-occur in plant communities, and the fourth covers hypothetical temporal dynamics of impacts by invasive N-fixing species.

RESULTS

1. Characteristics of the dataset

1.1 Study species

Among the studied genera, the most represented were *Acacia* (23%), *Lupinus* (14%), and *Lespedeza* (12.5%). 96% of the selected species were legumes, while actinorhizal N-fixers only made up 4%. 86% of the N-fixing species were classified as invasive in the studied range, while 14% were only classified as non-native species. Woody N-fixing species accounted for 60% of the pool of species, while herbaceous N-fixers made up 40% (Table 2).

Table 2: Invasive N-fixing species represented in the 48 studies (across the 45 papers) included in this review. For each species, the type of N-fixer (legume or actinorhizal), growth form (woody or non-woody), and associated studies are listed. Studies examining the same focal species are grouped within a single row, while studies including multiple invasive N-fixing species are represented across multiple rows.

Species	Type of N-fixer	Growth form	Associated paper(s)
Acacia auriculiformis	Legume	Woody	Yang et al. 2009;
Acacia dealbata	Legume	Woody	Fuentes-Ramírez et al. 2011; González-Muñoz et al. 2012; Lorenzo et al. 2017
Acacia longifolia	Legume	Woody	Marchante et al. 2003; Werner et al. 2010; Hellmann et al. 2011; Große-Stoltenberg et al. 2025
Acacia mangium	Legume	Woody	Yang et al. 2009; Meira-Neto et al. 2018

Acacia pycnantha	Legume	Woody	Lazzaro et al. 2015
Amorpha fructicosa	Legume	Woody	Boscutti et al. 2020; Vujanović et al. 2022
Cytisus scoparius	Legume	Woody	Watt et al. 2003; Shaben and Myers 2010; Allen et al. 2020; Parker and Harpole 2025
Falcataria moluccana	Legume	Woody	Hughes and Denslow 2005
Genista aetnensis (Biv.) DC.	Legume	Woody	Stinca et al. 2015
Lespedeza cuneata	Legume	Non-woody	Brandon et al. 2004; Fill et al. 2019; Garrett and Gibson et al. 2020; McMillan et al. 2023; Gholizadeh et al. 2024; Rakotoarivony et al. 2024
Lotus corniculatus	Legume	Non-woody	Oschrin and Reynolds 2019
Lupinus arboreus	Legume	Woody	Pickart et al. 1998
Lupinus nootkatensis	Legume	Non-woody	Hanslin and Kollmann 2016; Vetter et al. 2018
Lupinus polyphyllus	Legume	Non-woody	Thiele et al. 2010; Hansen et al. 2021; Prass et al. 2022; Lone et al. 2024
Melilotus alba	Legume	Non-woody	Spellman and Wurtz 2011
Melilotus officinalis	Legume	Non-woody	Van Riper and Larson 2009; Dornbusch et al. 2018; Ren et al. 2023
Myrica faya	Actinorhizal	Woody	Walker and Vitousek 1991; Adler et al. 1998
Prosipis (spp.)	Legume	Woody	Ndhlovu et al. 2016
Prosipis glandulosa	Legume	Woody	Archer et al. 1995; Iponga et al. 2010
Prosipis juliflora	Legume	Woody	Majumdar et al. 2025
Retama monosperma	Legume	Woody	Muñoz-Vallés et al. 2011; Esquivas et al. 2015
Sparticum junceum	Legume	Woody	Gavilán et al. 2016
Trifolium pratense	Legume	Non-woody	Ren et al. 2023
Trifolium repens	Legume	Non-	Ren et al. 2023

woody

1.2 Study systems

The geographical distribution of the examined studies was uneven, with 40% occurring in North America and 38% in Europe. In contrast, Asia was only represented by 9%, Africa by 4% (all occurring in South Africa), South America by 4%, and New Zealand by 4% (Figure 1).

Figure 1: Geographical distribution of experimental studies. All 45 studies are plotted using red dots on the map based on location of data collection.

In terms of ecological systems, grasslands were overrepresented in the sample, making up 35% of the study systems. Sand dunes (12%), woodlands (10%), and post-volcanic eruption sites (8%) were the next most common study systems. 10% of the examined studies were conducted in a greenhouse setting (Figure 2). More than 80% of the studies were conducted in systems reported as

low in nutrients or low in nitrogen. Of the remaining studies, only about 8% were in study systems explicitly described as low nutrient (Table 3).

Study system	Percent of papers
Grassland	35.29%
Dune	13.73%
Woodland	9.80%
Greenhouse	9.80%
Volcanic	7.84%
Savanna	5.88%
Forest	5.88%
Shrubland	3.92%
Floodplain	3.92%
Rangeland	1.96%
Heathland	1.96%
Total	**100.00%**

Grassland: open ecosystem dominated by grasses, sedges, and herbaceous plants

Sand dune: ridges of sand, characterized by low nutrient conditions and grass species

Woodland: forest habitat with an open canopy and a rich understory

Post-volcanic eruption: highly disturbed environment with underdeveloped soils

Figure 2: Relative frequency of study systems in the pool of selected literature. Percentages were calculated by dividing the occurrence of one type of system by the total number of study systems. The total number of study systems (48) exceeded the number of papers (45) given that several papers conducted data collection in multiple different systems.

Table 3: Proportion of studies conducted in low-nutrient systems. Greenhouse studies were categorized as N/A, and studies lacking sufficient information on soil nutrient status were classified as "Not reported."

Is the study system low-nutrient?	Percent of papers
Yes	80.39%
No	7.84%

N/A (greenhouse)	9.80%
Not reported	1.96%
Total	**100.00%**

1.3 Study methods

60% of studies were observational comparisons of community characteristics in invaded and uninvaded field locations. 40% of the studies involved experimental manipulation, either in the field or in a greenhouse (Table 4). The vast majority of selected studies were conducted over a short time period, with 87% carried out in one year or less. Only 4% of the studies were conducted over a period longer than 3 years (Table 4).

Table 4: Relative frequency of studies by method (experimental vs. observational) and, separately, by duration (years).

Study method	Percent of papers	Study duration	Percent of papers
Experimental	40.00%	0–1 years	86.67%
Observational	60.00%	1–3 years	8.89%
		> 3 years	4.44%
Total	**100.00%**	**Total**	**100.00%**

Changes to community biodiversity were documented using measures of species richness, the Shannon–Wiener Biodiversity Index, and functional diversity. 49% of the studies included a measure of species richness, while Shannon–Wiener Biodiversity Index (15%) and functional diversity (7%) were

less commonly used. Changes to community density were calculated using measures of biomass and percent cover, with 38% of studies including a measure of biomass and 29% including a measure of cover. 24% of all studies documented a change in community composition. 29% of all studies differentiated between measures of native and non-native biodiversity and density.

2. Pathways results

2.1 Facilitation

Table 5: Facilitation pathways identified in this review, with the number of supporting studies and corresponding literature for each pathway.

Pathway	Number of papers	Supporting literature
1a. Invasional meltdown (preferential facilitation of other invasive species): co-invasions	12	Archer et al. 1995; Hughes and Denslow 2005; Iponga et al. 2010; Shaben and Myers 2010; González-Muñoz et al. 2012; Oschrin and Reynolds 2019; Allen et al. 2020; Vujanović et al. 2022; Ren et al. 2023; Lone et a 2024; Majumdar et al. 2025; Parker and Harpole 2025
1b. Invasional meltdown (preferential facilitation of other invasive species): death of N-fixer	3	Adler et al. 1998; Pickart et al. 1998; Dornbusch et al. 2018
2. Facilitation of functional group: preferential facilitation of particular functional groups, typically nitrophilous ruderal species.	9	Thiele et al. 2010; Hellmann et al. 2011; Muñoz Vallés et al. 2011; Gavilán et al. 2016; Ndhlovu et al. 2016; Vetter et al. 2018; Fill et al. 2019; Boscutti et al. 2020; Hansen et al. 2021
3. Self-facilitation: habitat alteration by an invasive N-fixer can act as a self-reinforcing process, driving dominance of the N-fixer in the community.	4	Marchante et al. 2003; Hellmann et al. 2011; Lorenzo et al. 2017; Meira-Neto et al. 2018

4. Blanket facilitation: non-preferential facilitation, impacting most species in the system	7	Van Riper and Larson 2009; Yang et al. 2009; Stinca et al. 2015; Hanslin and Kollmann 2016; Meira-Neto et al. 2018; Vetter et al. 2018; Rakotoarivony et al. 2024

2.2 Competition

Table 6: Competition pathways identified in this review, with the number of supporting studies and corresponding literature for each pathway.

Pathway	**Number of papers**	**Supporting literature**
1a. Novel growth strategy/structure: invasive N-fixer has a competitive advantage due to a growth strategy/structure that differs from that of the recipient community	12	Marchante et al. 2003; Brandon et al. 2004; Van Riper and Larson 2009; Fuentes-Ramírez et al. 2011; Spellman and Wurtz 2011; Esquivias et al. 2015; Meira-Neto et al. 2018; Garrett and Gibson 2020; Hansen et al. 2021; Prass et al. 2022; McMillan et al. 2023; Große-Stoltenberg et al. 2025; Majumdar et al. 2025
1b. Novel resource use: invasive N-fixer has a competitive advantage due to a resource use trait that differs from that of the recipient community	5	Watt et al. 2003; Shaben and Myers 2010; Werner et al. 2010; Esquivias et al. 2015; Meira-Neto et al. 2018

FACILITATION PATHWAYS

In this section, I outline common categories of facilitative interactions involving invasive N-fixing plants in plant communities. As discussed previously, positive plant–plant interactions often arise when a "benefactor" species modifies the environment in ways that improve growth of other species (Bruno et al. 2003; McIntire and Fajardo 2013). N-fixing plants are particularly strong facilitators because their symbiotic association with nitrogen-fixing bacteria often increases the availability of nitrogen, a key limiting nutrient in many terrestrial systems (Vitousek and Howarth 1991; Bonanomi et al. 2011).

As a result, the facilitative pathways considered here are primarily mediated by changes to nitrogen cycling. In nutrient-limited systems, increases in nitrogen availability often have broadly positive effects on plant growth (Callaway 2007). In this sense, facilitation via nitrogen enrichment can also be understood as a reduction in competition for nitrogen, as the limiting resource becomes more available (Callaway and Walker 1997).

However, the effects of invasive N-fixers are rarely limited to nitrogen enrichment alone. In addition to increasing soil nitrogen, these species often modify other aspects of the environment, including microclimate, soil structure, and moisture availability (Ehrenfeld 2003). One common example in the literature is the formation of "islands of fertility" beneath the canopies of woody N-fixers (Schlesinger and Pilmansis 1998; Bonanomi et al. 2011; Stinca et al. 2015). These patches are characterized by elevated nutrient availability, greater soil organic

matter, more stable temperatures, and increased moisture retention, creating localized areas of improved growing conditions (Schlesinger and Pilmansis 1998; Stinca et al. 2015).

Across the literature in this section, nitrogen enrichment is the consistent driver of facilitation, often acting in combination with other forms of habitat modification (Ortiz and Wolf 2024). As a result, variation among pathways largely reflects differences in which species or groups benefit from these changes, rather than how facilitation occurs, which always involves N-enrichment in some form.

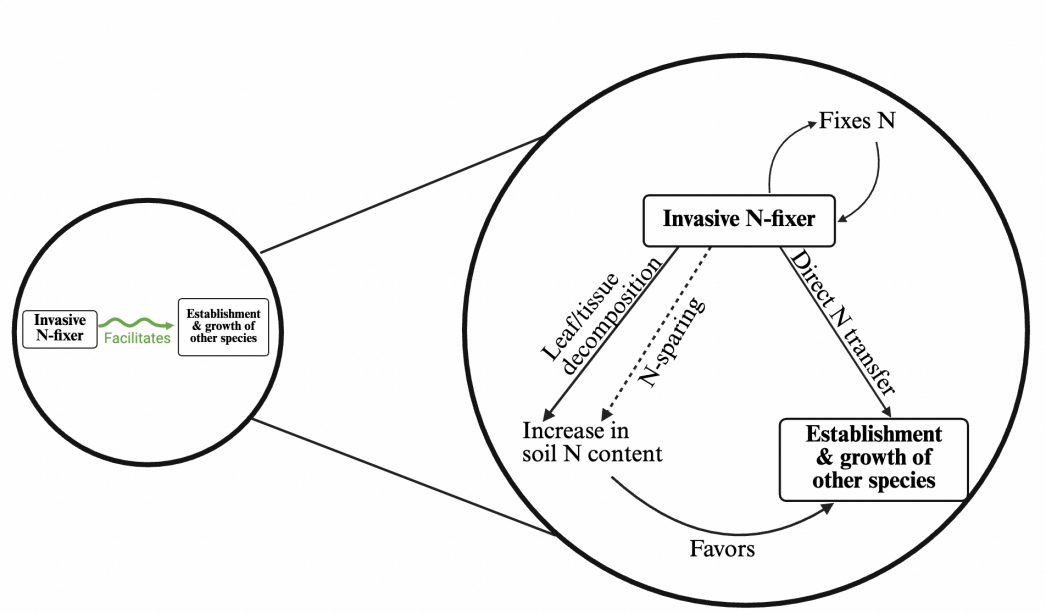

Figure 3: Conceptual diagram illustrating the mechanisms of facilitation by invasive N-fixing plants, as indicated in the literature. The green arrow denotes facilitative interactions and is used as a visual shorthand in subsequent figures. Figure was created with BioRender.

1. Invasional meltdown

This pathway encompasses cases where invasive N-fixing plants preferentially facilitate other invasive species, amplifying invasion impacts within the community.

The process by which one invasive species facilitates the establishment, survival, or growth of a suite of other invaders is called “invasional meltdown” (Simberloff and Van Holle 1999). Invasive N-fixers are strong drivers of invasional meltdown, largely because the ecosystem alterations associated with nitrogen fixation are particularly conducive to the establishment and growth of invading species (Oschrin and Reynolds 2019; Lone et al. 2024). This pattern aligns with Mark Davis’ fluctuating resource hypothesis, which posits that plant communities become more susceptible to invasion following an increase in the amount of unused resources in a system (Davis et al. 2000). This theory is particularly true when the availability of a limiting resource increases (Davis et al. 2000). Therefore, invasion and subsequent nitrogen enrichment by an N-fixing species in a nutrient-limited environment creates increased variation in resource availability, which favors the growth of invading species (Simberloff and Van Holle 1999; Davis et al. 2000; Lone et al. 2024). A majority of invasive species often have traits associated with higher nutrient-use efficiency and fast vegetative growth, meaning that they can better take advantage of the heightened nitrogen content compared to native species (Funk and Vitousek 2007; Pyšek and Richardson 2007). In theory, invasional meltdown results in an accumulation of

invaders and their impacts and the gradual displacement of native species from the community (Simberloff and Van Holle 1999; Ricciardi and Simberloff 2025).

In practice, this facilitation tends to occur in two ways: by increasing the biomass of existing invasive species or by enabling the establishment of new ones. Increased growth of existing invaders can shift competitive dynamics, often giving them an advantage over native species (Adler et al. 1998; Dornbusch et al. 2018). Alternatively, nutrient enrichment can remove environmental filters that previously prevented establishment, increasing invasive species richness (Schöb et al. 2012; O'Brien et al. 2019).

1a. Co-invasion

In invasional meltdown, co-invasions occur when two or more invasive species are present in a system, and interact to generate combined impacts (Figure 4; Ahmad et al. 2025; Oschrin and Reynolds 2019). Thus, both the invasive N-fixer and the facilitated species can be understood as simultaneous drivers of community change (Oschrin and Reynolds 2019; Lone et al. 2024). The mechanisms underlying impacts from co-invasions must therefore be attributed both to the individual mechanisms of impact of each invasive species, as well as interactions between the species (Ahmad et al. 2025).

Co-invasions can result in an amplification of the impacts of the invading species (Oschrin and Reynolds 2019; Lone et al. 2024; Ahmad et al. 2025). These synergistic effects occur when the overall magnitude of impact of the co-invasion

is greater than the sum of the effects of individual invaders (Oschrin and Reynolds 2019; Ahmad et al. 2025), and are more likely to occur when the underlying mechanisms of invasion and impact differ between the invasive species (Tekiela and Barney 2017). For example, Vujanović et al. (2022) conducted a greenhouse study with three co-occurring invaders, one of which was a N-fixing legume. The three species had differing traits associated with impact, namely allelopathy, nitrogen-fixation, and the formation of dense thickets. Vujanović et al. (2022) found a greater negative impact on native species diversity when the invaders were grown together than the sum of their impacts when grown individually. Facilitation played a key role in generating this synergistic effect, as nitrogen enrichment from the invasive N-fixer promoted biomass production of the co-invaders, thus strengthening their effect on the native species (Vujanović et al. 2022).

Synergies can also arise through reinforcing feedbacks (Ehrenfeld et al. 2005). In invasions by N-fixing species, this typically occurs when the N-fixer and facilitated species generate a positive plant–soil feedback cycle, substantially increasing nitrogen cycling in the system (Simberloff and Van Holle 1999; Ehrenfeld et al. 2005). For example, Dornbusch et al. (2018) and Adler et al. (1998) found that the natural decomposition of facilitated invasive grasses contributed additional nitrogen to the soil, effectively amplifying the impact of the invasive N-fixer on nitrogen cycling. This served to maintain the dominance of both the invasive N-fixer and the invasive grasses in the systems. While the

synergistic effects occur through alterations of plant–soil feedbacks, which are not a direct community impact, the resulting nutrient enrichment leads to the reinforcement of the co-invading species populations (Adler et al. 1998; Toledo et al. 2014). This has the potential to shift the community towards one dominated by invasive and non-native species (Adler et al. 1998; Dornbusch et al. 2018).

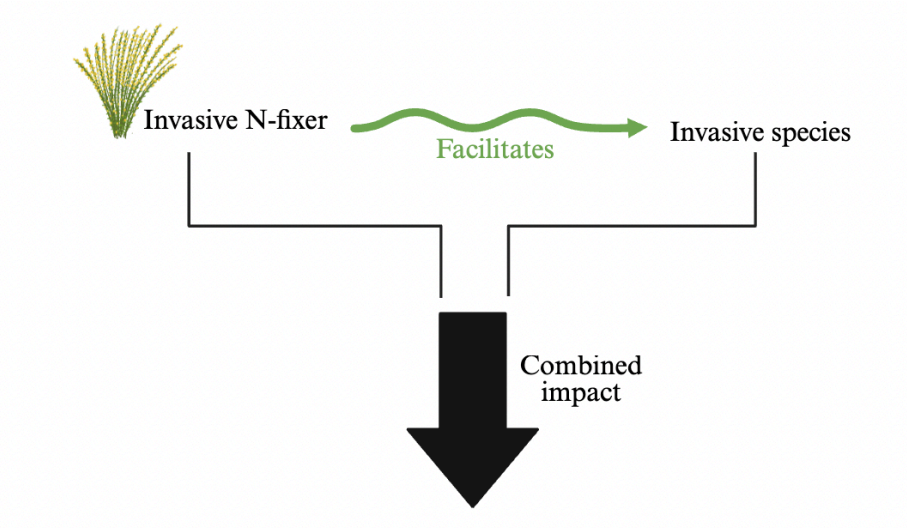

Figure 4: Conceptual diagram of co-invasion, in which an invasive N-fixing species facilitates a second invasive species, resulting in a combined impact on the community. The green arrow denotes facilitation. Figure was created with BioRender.

1b. Death of the N-fixer

Interactions between co-occurring invasive species in a system are not always positive; competition between invasive species is common, and can lessen the overall impact on the community (Ahmad et al. 2025). In instances where co-occurring invaders have antagonistic effects, an invasive N-fixer may only facilitate another invasive species after its death. In this pathway, the N-fixing

species creates a point of entry for other invading species by dying, decomposing, and leaving behind an open patch of nutrient-rich soil (Figure 5; Adler et al. 1998; Pickart et al. 1998; Dornbusch et al. 2018). Unlike co-invasion, the species do not generate combined impacts.

The facilitated invasive species benefit in two main ways. First, death of the invasive N-fixer creates a niche opportunity, where fast-establishing invasive species can colonize open space without competition from either the N-fixer or surrounding vegetation (Shea and Chesson 2002; Hess et al. 2019). Second, these patches are often high in available nitrogen due to decomposition, which further promotes growth (Adler et al. 1998; Pickart et al. 1998). Experimental work has shown that soil nitrogen can even be higher following the death of the N-fixer than under the live plant (Pickart et al. 1998; Weil and Brady 2017). Together, these factors can give invasive species a strong establishment and growth advantage over native species in the community (Adler et al. 1998; Dornbusch et al. 2018).

A clear example of this pathway comes from Adler et al. (1998), who examined insect-driven dieback of the invasive N-fixing tree *Myrica faya*. Following dieback, the authors observed a substantial increase in invasive grass cover in the system. These grasses were able to rapidly colonize the nutrient-rich patches left behind by the dying trees, benefiting both from reduced competition and increased nitrogen availability. Over time, this shift in vegetation altered the disturbance regime as well. The invasive grasses were highly flammable and

quick to regrow after fires. The increased cover was predicted to lead to more frequent and severe fires, ultimately generating a positive feedback in which the system shifted towards a non-native dominated grassland (D'Antonio and Vitousek 1992; Adler et al. 1998). In this case, although the initial driver of change was the invasive N-fixer, the longer-term community and ecosystem impacts were largely driven by the facilitated invader.

Because most of the studies used to describe this pathway were conducted over short timescales or in controlled settings, the long-term dynamics of these interactions are less well understood. However, several possible trajectories have been suggested. One is the eventual dominance of the facilitated invasive species, accompanied by a decline in the N-fixer, as seen in the *M. faya* study (Adler et al. 1998).

Alternatively, the plant death and facilitation might continue in a cyclical fashion, maintaining the presence of both invasive N-fixer and the facilitated invasive species in the system at different times (Figure 5; Maron and Jeffries 1999; Carino and Daehler 2002). In these systems, patches created by plant death are repeatedly colonized and vacated, allowing both species to persist over time. This trajectory is likely more common when the N-fixer and the facilitated species are both annual or short-lived (Maron and Connors 1996; Dornbusch et al. 2018). While this pattern has not been directly observed for invasive N-fixers in the literature reviewed here, work by Maron and Jefferies (1999) on a native N-fixing shrub provides a useful analogue. They found that invasive annual grasses

colonized nutrient-rich patches following shrub death, but that the shrub later re-established from the seed bank once the grasses completed their life cycle. This resulted in a cycle of plant death and re-establishment that maintained both species in the system.

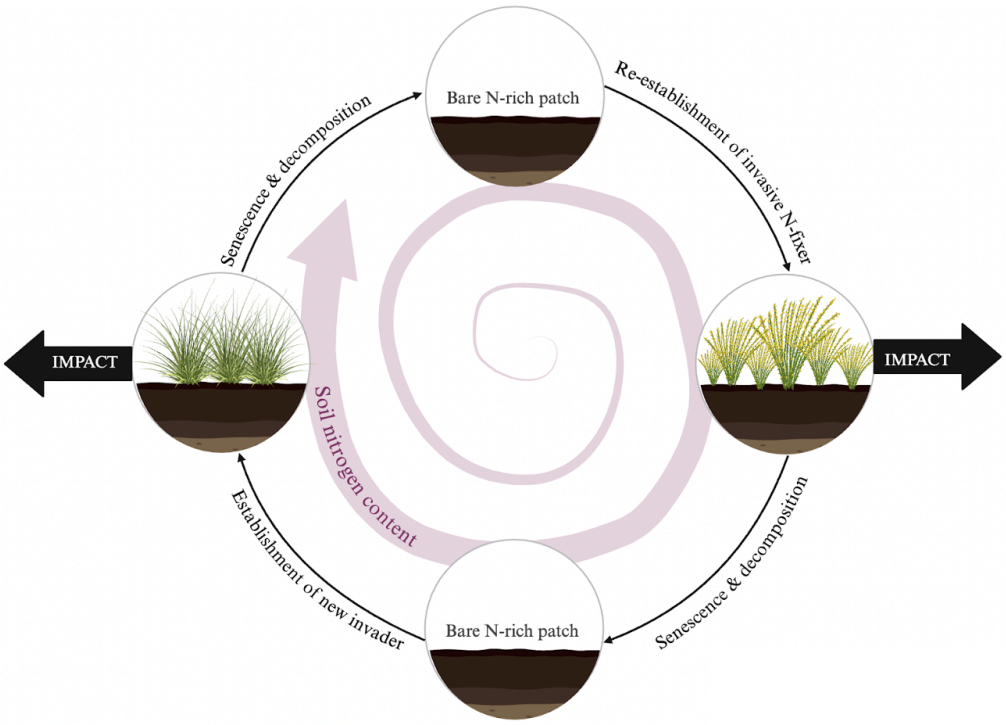

Figure 5: Conceptual diagram illustrating the cyclical dynamics of plant death and re-establishment between an invasive N-fixing plant and a facilitated invader. The pink arrow indicates the progressive increase in soil nitrogen content over the course of invasion and its feedback through repeated cycles of plant mortality and re-establishment. Black arrows represent the individual impacts of each invader. Figure was created with BioRender.

2. Preferential facilitation of functional groups

Invasive N-fixing plants may instead preferentially facilitate a particular functional group (Figure 6; Thiele et al. 2010; Hellmann et al. 2011; Muñoz Vallés et al. 2011; Gavilán et al. 2016; Ndhlovu et al. 2016; Vetter et al. 2018; Fill et al. 2019; Boscutti et al. 2020; Hansen et al. 2021). The nutrient alterations associated with N-fixing species can positively impact the establishment and growth of species with particular functional traits, regardless of native or non-native status. Typically, these species have traits that make them superior competitors under the conditions created by the invasive N-fixer (Hansen et al. 2021).

Here, functional traits refers to the characteristics involved in the ecological role of a species in its community, while a functional group is a category of species with similar functional traits (Marchetti et al. 2023). Across the studies reviewed, invasive N-fixers typically facilitate species with traits associated with high nitrogen uptake, fast growth, and tolerance for disturbance (Gavilán et al. 2016; Fill et al. 2019; Boscutti et al. 2020). These are described as nitrophilous ruderal species, and are commonly grasses (Hobbs and Huenneke 1992; Moreau et al. 2014).

In the low-nutrient systems that make up the majority of the study systems in this pathway, invasion by N-fixing species and subsequent nutrient enrichment effectively act as a disturbance, shifting resource availability in a way that favors these functional groups (Hobbes and Huenekke 1992). The species facilitated by

this disturbance are particularly adept at acquiring available soil nitrogen, allowing them to grow quickly and compete successfully with other existing plants for water, light, and other nutrients (D'Antonio and Vitousek 1992; Shaben and Myers 2010). In some cases, the facilitated species are also functionally distinct from the N-fixer (e.g., woody vs. herbaceous), which can reduce direct competition and further promote their success (Callaway 2007; Gavilán et al. 2016; Boscutti et al. 2020).

A clear example of this pathway comes from Fill et al. (2019), who examined the effects of the invasive N-fixer *Lespedeza cuneata*. In this system, nutrient enrichment from *L. cuneata* facilitated perennial grasses, increasing their biomass. These grasses then exerted a competitive effect on native forbs, reducing their density. Importantly, *L. cuneata* did not directly suppress the forb species. Instead, it altered competitive dynamics within the community by facilitating a functional group that was better able to dominate under high-nitrogen conditions. This illustrates how facilitation can indirectly drive community change by shifting the balance of competition among species.

Similar patterns have been observed across a range of systems, where invasion by N-fixers leads to communities dominated by nitrophilous, fast-growing species (Thiele et al. 2010; Gavilán et al. 2016; Ndhlovu et al. 2016; Vetter et al. 2018; Boscutti et al. 2020). In some cases, this shift is accompanied by a decrease in functional richness, reflecting a loss of diversity in ecological strategies (Boscutti et al. 2020). In others, nutrient enrichment allows entirely new

functional groups to establish in the system, representing a form of niche construction by the invasive N-fixer (Fei et al. 2014; Vetter et al. 2018).

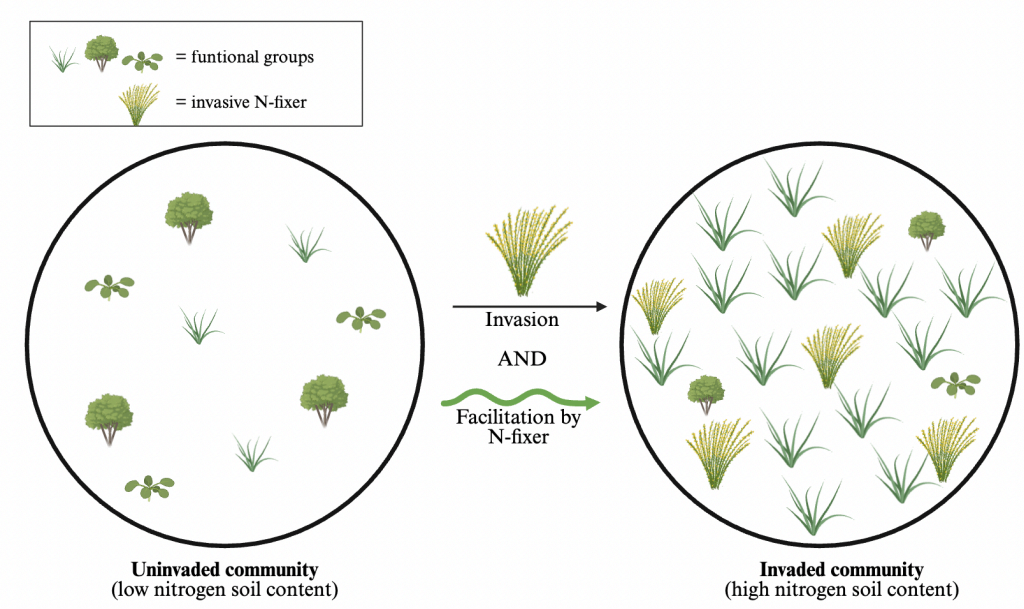

Figure 6: Conceptual diagram illustrating the preferential facilitation of a specific plant functional group by an invasive N-fixing species. Each unique symbol represents a distinct functional group. Increases in symbol size reflect increases in biomass, while increases in symbol frequency represent increases in plant density. Figure was created with BioRender.

3. Self-facilitation

Habitat alteration by an invasive N-fixer can act as a self-reinforcing process, driving dominance of the N-fixer in the community (Figure 7; Wilson and Agnew 1992; Callaway 2007). This occurs when seedlings of an invasive N-fixer have an advantage either establishing or growing in soils modified by the

plant itself. Most often, the seedlings benefit from elevated soil nitrogen, the increased presence of symbiotic Rhizobial bacteria, and higher water retention (Marchante et al. 2003; Hellmann et al. 2011; Lorenzo et al. 2017).

This pathway generates a positive feedback cycle: the N-fixer alters the environment, facilitates its own seedlings, and those individuals further modify the environment (Figure 7; Yelenik and D'Antonio 2013). These kinds of positive feedbacks, in which the outcome of a process increases the magnitude of the same process, can lead to cascading changes to the system if unchecked (Ehrenfeld 2005). Self-facilitation tends to result in the formation of dense, monospecific stands of the invasive N-fixing plant (Marchante et al. 2003; Hellmann et al. 2011; Lorenzo et al. 2017; Meira-Neto et al. 2018). These dense stands have the added effect of reducing light availability for the native vegetation, giving the invasive N-fixer competitive superiority in light capture (Marchante et al. 2003; Hellmann et al. 2011; Lorenzo et al. 2017; Meira-Neto et al. 2018). Dominance of the invasive N-fixer also prevents re-colonization by native species (Fuentes-Ramírez et al. 2011). Essentially, these self-facilitating patterns can shift the community towards competition over light and space, maintaining the dominance of the invader in the system (Grime 2002; Yelenik and D'Antonio 2013).

As is clear in the previous facilitation pathways, nutrient enrichment and habitat modification do not always result in only the dominance of the invasive N-fixer. For an increase in soil nitrogen content to confer a competitive advantage

to the N-fixer, self-facilitation must outweigh facilitation of other species in some way (Yelenik and D'Antonio 2013; Lorenzo et al. 2017). Based on the literature, the balance of this outcome is primarily a function of seed output and germination timing. Hellmann et al. (2011) found that the invasive N-fixer *Acacia longifolia* produced seeds at both a higher rate and earlier in the season compared to the native vegetation. The seedling growth was enhanced by the higher nutrient content and soil stabilization provided by the tree roots (Hellmann et al. 2011). Combined, these factors meant that *A. longifolia* seedlings prevented native species from establishing below and directly around the canopy of the mature trees (Hellmann et al. 2011).

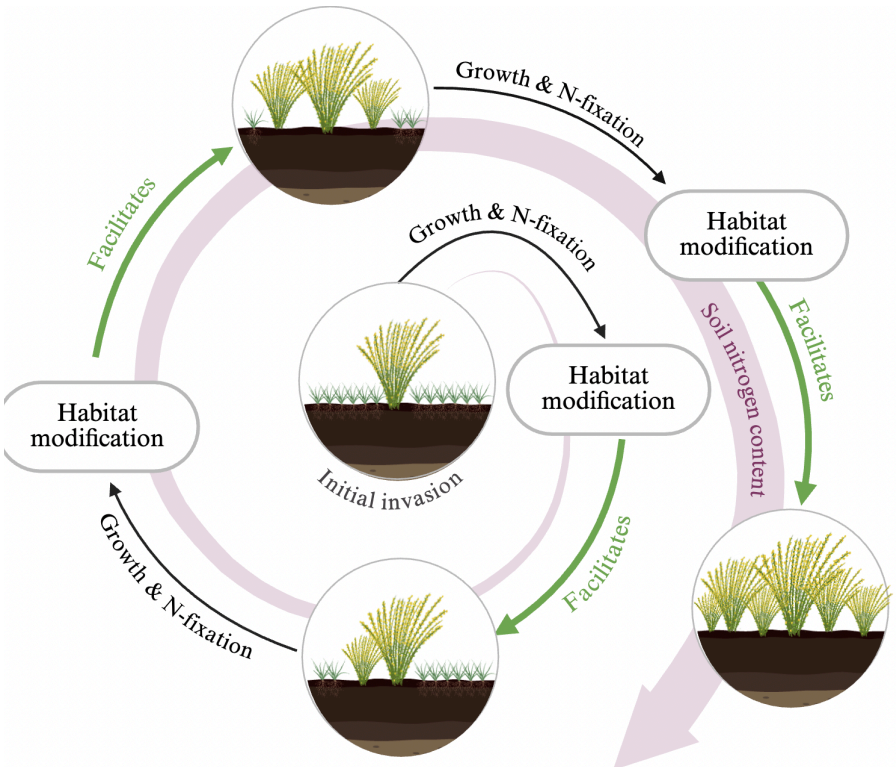

Figure 7: Conceptual diagram illustrating a self-facilitating positive feedback loop in invasive N-fixing species. Increases in symbol size indicate increases in

biomass, while increases in symbol frequency represent higher plant density. The pink arrow represents increasing soil nitrogen content over time, and green arrows denote facilitative interactions. Figure was created with BioRender.

4. Blanket facilitation

In contrast to preferential facilitation, some invasive N-fixing species generate broadly positive effects across the entire plant community (Figure 8; Van Riper and Larson 2009; Yang et al. 2009; Stinca et al. 2015; Hanslin and Kollman 2016; Meira-Neto et al. 2018; Vetter et al. 2018; Rakotoarivony et al. 2024).

The study by Stinca et al. (2015) provides an example of this pattern, as well as insight into the conditions under which blanket facilitation may occur. They examined invasion by the N-fixing shrub *Genista aetnensis* on the Vesuvius Grand Cone. Although the study took place decades after the eruption of Mt. Vesuvius, the soils remained sandy, nutrient-poor, and low in water-holding capacity. As one of the few species capable of establishing under these harsh conditions, *G. aetnensis* gradually generated localized patches of elevated nitrogen and organic carbon beneath its canopy through leaf litter decomposition.

In addition to nutrient enrichment, *G. aetnensis* ameliorated multiple abiotic stressors. Its large canopy buffered extreme soil surface temperatures and reduced evaporative water loss, increasing soil moisture retention. Together, these habitat modifications enhanced plant colonization on the otherwise barren slopes, particularly beneath the canopy. This resulted in increases in both native species richness and total biomass. Importantly, there was no clear evidence of

preferential facilitation of particular functional groups or non-native species, although some non-native species did benefit from these changes (Stinca et al. 2015).

A common thread across many of the studies in this pathway is the role of invasive N-fixers in soil development. Many systems were characterized by severely degraded, disturbed, or early-successional soils with low nutrient availability (Yang et al. 2009; Stinca et al. 2015; Hanslin and Kollman 2016). In these contexts, the researchers described nitrogen fixation and associated habitat modifications as rapidly increasing the availability of key resources, making the soil more fertile for all species present (Hanslin and Kollman 2016). Nitrogen-fixing plants are well known for their role in early soil development, often facilitating subsequent colonization by other species through dramatic increases in nitrogen inputs (Vitousek and Walker 1989). Under conditions of high abiotic stress, this kind of stress amelioration may broadly benefit the entire community (Bertness and Callaway 1994).

However, as Stinca et al. (2015) note, this blanket facilitation may not persist as the community changes. As the biomass of all the species in the system increases, new competitive dynamics may emerge as space becomes more of a limiting resource (Grams and Lüttge 2010). And, as the nature of the substrate, resource availability, and growing conditions changes in the system, often becoming less stressful for the present vegetation, the environmental filters preventing the establishment of resource-demanding nitrophilous species may

lessen (Stinca et al. 2015). Stinca et al. (2015) suggest that the blanket facilitation they observed may shift toward preferential facilitation as existing non-native species gain a competitive advantage under the new resource conditions. In this sense, blanket facilitation may represent an early stage in a longer trajectory of community change.

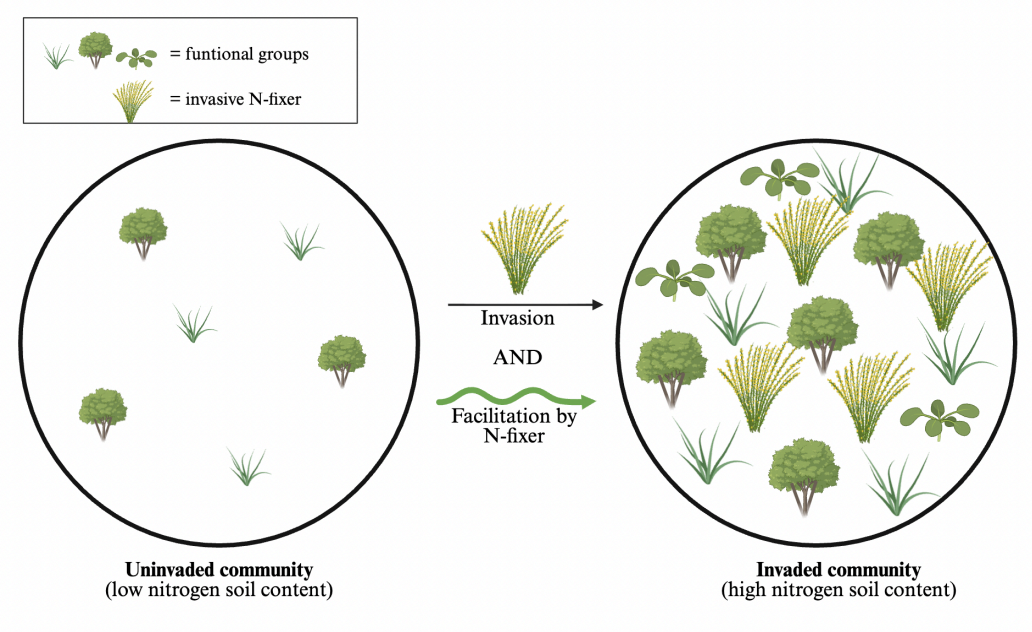

Figure 8: Conceptual diagram illustrating the non-preferential facilitation of plants in a community by an invasive N-fixing species. Each unique symbol represents a distinct functional group. Increases in symbol size reflect increases in biomass, while increases in symbol frequency represent increases in plant density. Figure was created with BioRender.

COMPETITION PATHWAYS

As discussed earlier, competitive interactions are mediated by access to a shared limiting resource (Marchetti et al. 2023). In outlining pathways of competition leading to community change, it is necessary to identify both what the limiting resources are and how invasive N-fixers are able to access them more effectively than native species.

Contrary to what might be expected, the literature tends to agree that nitrogen itself is often not the resource over which invasive N-fixers compete with native species (Watt et al. 2003; Brandon et al. 2004; Werner et al. 2010). Instead, invasion by an N-fixing plant was typically associated with a shift in the identity of the limiting resource (Funk and Vitousek 2007). By increasing the availability of nitrogen in the system, the N-fixer reduces its importance as a limiting factor and elevates the importance of other resources such as light, water, or space (Watt et al. 2003; Brandon et al. 2004; Werner et al. 2010). Therefore, the competitive interactions covered in this review are mediated by those resources, and not nitrogen.

In this way, invasion by an N-fixing plant alters the resource landscape of the system, effectively introducing new competitive dynamics. Because competition is mediated by a limiting resource, changing the availability of one resource can fundamentally reorganize competitive interactions and hierarchies (Marchetti et al. 2023). Habitat modifications by the invader, such as canopy formation or changes to nutrient cycling, drive this shift in identity of the limiting

resource (Funk and Vitousek 2007). As a result, invasive N-fixers often gain a competitive advantage not by outcompeting native species for nitrogen, but by being superior competitors for a newly limiting resource (Brandon et al. 2004; Werner et al. 2010).

Nitrogen fixation and its impact on nutrient cycling still underlies these interactions, but indirectly. Nitrogen fixation gives these plants the ability to invade and establish in resource-limited environments, and it often drives the changes to the resource environment associated with the invader (Walker and Vitousek 1989; Funk and Vitousek 2007).

The competition pathways outlined here focus on the traits and mechanisms that allow invasive N-fixers to access limiting resources more effectively than native species. The key distinction between pathways lies in the type of resource being competed for and the mechanisms by which competitive advantage is achieved.

1. Introduction of novel traits

It is important to recognize that the traits that confer competitive ability differ substantially between low- and high-nutrient environments (Funk 2013). This distinction is central to understanding competition involving invasive N-fixing plants. Most of the invasions examined in this review occur in nutrient-limited systems (Table 4), where native species tend to exhibit traits

associated with resource conservation (Funk and Vitousek 2007). These include long leaf lifespans, low tissue nutrient content, slow growth rates, and relatively small stature (Vitousek 1982; Funk and Vitousek 2007). These traits allow plants to persist under chronic nutrient limitation—making them successful competitors in low-nutrient environments—but do not support rapid resource acquisition or growth (Funk 2013).

In contrast, because N-fixing plants are not limited by nitrogen, they are able to adopt growth and resource-use strategies more typical of species in nutrient-rich environments (Xiao et al. 2024). These strategies include greater allocation to aboveground biomass, higher specific leaf area, faster growth rates, and higher photosynthetic capacity (Xiao et al. 2024). Under high-nutrient conditions, these traits confer strong competitive ability.

This creates a mismatch when N-fixing plants invade nutrient-poor systems. A species with traits associated with high resource availability is able to establish within a community composed of species adapted to resource limitation. Because the N-fixer can access atmospheric nitrogen, it is not constrained by the same trade-offs that shape native species strategies (Funk and Vitousek 2007; Scherer-Lorenzen et al. 2007). As a result, it can maintain a high resource-use strategy even in environments where such strategies are typically not viable (Funk and Vitousek 2007). These traits—particularly those related to growth rate, structure, and resource use—can shift competitive dynamics by altering both the identity of the limiting resource and the traits required for competitive success.

1a. Novel growth strategy or structure

This pathway encompasses interactions where the invasive N-fixer has a competitive advantage due to a growth-related strategy or trait that differs from that of the recipient community (Figure 9; Marchante et al. 2003; Brandon et al. 2004; Fuentes-Ramírez et al. 2011; Esquivas et al. 2015; Meira-Neto et al. 2018; Garrett and Gibson et al. 2020; Hansen et al. 2021; McMillan et al. 2023; Große-Stoltenberg 2025). In general, these interactions alter the availability of light or space, often shifting the limiting resource to one of these factors and displacing native species (Funk and Vitousek 2007; Hellmann et al. 2016; Ndhlovu et al. 2016).

Many invasive N-fixers in this pathway exhibit faster growth rates and larger leaf sizes relative to surrounding vegetation (Marchante et al. 2003; Brandon et al. 2004; Fuentes-Ramírez et al. 2011; Esquivas et al. 2015; Garrett and Gibson et al. 2020; Hansen et al. 2021; McMillan et al. 2023; Große-Stoltenberg 2025;). As a result, they can rapidly occupy space and outcompete native species through shading or physical displacement (Brandon et al. 2004; Garrett and Gibson et al. 2020). For example, in a nutrient-poor grassland environment, the invasive legume *Lespedeza cuneata* outcompeted native vegetation by quickly forming tall, dense stands that blocked light capture for species below (Brandon et al. 2004).

Invasive N-fixers may also introduce novel growth structures to the system (Marchante et al. 2003; Brandon et al. 2004; Fuentes-Ramírez et al. 2011; Große-Stoltenberg 2025). This is frequently paired with the growth strategies covered above. If an invasive N-fixer forms a canopy taller than the existing vegetation, it can easily out compete native species for light (Hellmann et al. 2016). For instance, Marchante et al. (2003) found that the invasive tree *Acacia longifolia* had a taller stature than dune-adapted native species, effectively creating a new vegetation layer with a dense canopy that reduced access to light for native species (Marchante et al. 2003). Even if the native species were able to benefit from the increased soil nitrogen below the tree, both Marchante et al. (2003) and Esquivas et al. (2015) suggest that they may have to allocate the additional nitrogen towards producing more chlorophyll to deal with the effects of shading.

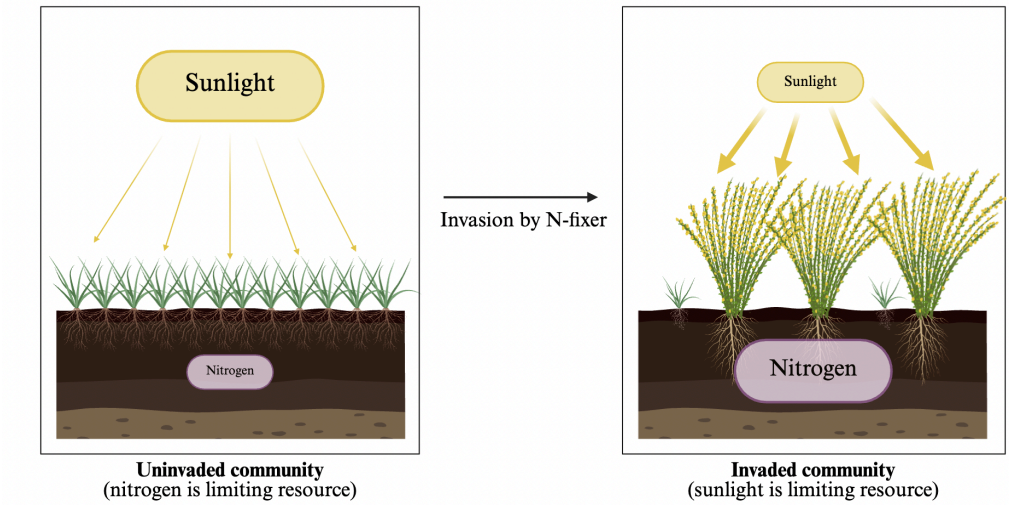

Figure 9: Conceptual diagram illustrating the competitive effects of an invasive N-fixing species with a novel growth structure on native vegetation. Small grass

symbols represent native plants, while larger yellow shrub symbols represent the invasive N-fixer. The relative sizes of the sunlight and nitrogen symbols indicate their availability within the system. Arrows represent uptake of the resources, with thicker arrows indicating higher uptake. Figure was created with BioRender.

1b. Novel resource use trait

This pathway encompasses instances where invasive N-fixers introduce novel patterns of resource use (Figure 10). Some invasive N-fixers function as resource-demanding species, requiring high quantities of resources and allocating them toward rapid growth (Craine and Dybzinski 2013). In the literature, these species are often characterized by high uptake of water or phosphorus, effectively shifting limitation toward those resources (Watt et al. 2003; Shaben and Myers 2010; Werner et al. 2010; Esquivas et al. 2015; Meira-Neto et al. 2018).

These traits are typically not advantageous in resource-limited environments, and it is unusual for resource-demanding species to invade low-nutrient systems (Funk and Vitousek 2007; Funk 2013). However, nitrogen fixation allows these species to establish while maintaining high rates of resource use for other limiting factors.

In general, these kinds of invasions are characterized by a lack of plasticity on the part of the invasive N-fixer, given that the plant does not reduce its high resource usage even in a low resource environment (Werner et al. 2010). For example, Werner et al. (2010) found that the resource-demanding invasive legume *Acacia longifolia* was a successful competitor in Mediterranean sand dunes that were both nutrient-poor and drought prone. Although *A. longifolia* is

not adapted to the Mediterranean environment, the N-fixer was still able to achieve high resource allocation towards growth and rapid biomass accumulation, largely attributed to its ability to fix nitrogen (Werner et al. 2010). *A. longifolia* also had high water consumption, which lowered water cycling in the system and generated a negative effect on the native species (Werner et al. 2010). The N-fixers took up comparatively more of those resources than native species, which reduced the availability of those resources for use by the native species.

High uptake of another limiting resource can outweigh any positive effects of nitrogen enrichment (Watt et al. 2003). For example, the invasive N-fixer *Cytisus scoparius* had an overall negative effect on *Pinus radiata* in an arid environment by significantly reducing water availability. Although some direct nitrogen transfer occurred, this benefit was outweighed by the negative effects of water limitation (Watt et al. 2003). This dynamic is especially likely in systems where water or light, rather than nitrogen, ultimately constrains growth.

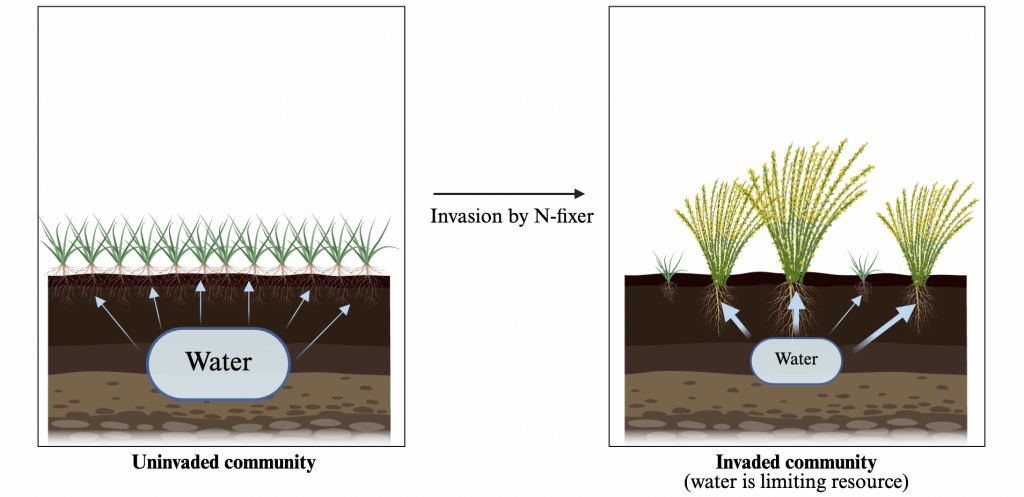

Figure 10: Conceptual diagram illustrating the competitive effects of an invasive N-fixing species with a novel resource use trait on native vegetation. Small grass symbols represent native plants, while larger yellow shrub symbols represent the invasive N-fixer. The relative size of the water symbols indicates its availability within the system. Arrows represent uptake of the resource, with thicker arrows indicating higher uptake. Figure was created with BioRender.

CO-OCCURRING COMPETITION AND FACILITATION

In the previous section, I outlined categories of facilitative and competitive interactions as mostly independent phenomena. Isolating interactions and their effects reflects much of the literature reviewed here and is a useful approach to identifying how that interaction results in a community change (Callaway and Walker 1997). Many foundational theories on species interactions and their role in community structure were initially developed from studies that looked at the interactions as independent phenomena (Connell 1983; Hunter and Aarsson 1988; Callaway and Walker 1997). It would be difficult to make sense of the complex combinations of interactions within a community without first defining these pieces, and the same is true for approaching impacts of invasive N-fixers.

However, in reality, facilitative interactions and competitive interactions do not exist in a vacuum. Community changes are often a product of co-occurring, frequently simultaneous, facilitative and competitive interactions (Callaway and Walker 1997; Callaway 2007; Ortiz and Wolf 2024). Therefore, a more comprehensive understanding of community structure and change requires examining not only individual interactions, but also the interplay between facilitative and competitive forces and the conditions under which they occur. Some researchers have found that documenting networks of interacting

mechanisms, rather than focusing on a single causative pathway, is a more promising approach to understanding mechanisms of invasive species impacts (Ehrenfeld 2010; Simberloff 2010). Invasive N-fixing plants are particularly interesting to explore from this perspective. It is apparent from the pathways section of this thesis that N-fixation gives these invaders the potential for both facilitation and competition, and so it is a logical next step to assume that both types of interactions may occur simultaneously in the invaded communities.

1. Case study: Ndhlovu et al. 2016

One way to make sense of this complexity is to imagine the individual interaction pathways as building blocks. Each pathway represents a distinct mechanism, but community-level outcomes emerge from how those blocks combine. The study by Ndhlovu et al. (2016) on invasive leguminous trees in the *Prosipis* genus in South African rangeland environments provides an excellent example of this co-occurrance of competition and facilitation. The researchers were not able to identify individuals beyond the genus level due to lack of information on *Prosipis* species classifications in South Africa (Ndhlovu et al. 2011; Ndhlovu et al. 2016).

Prosipis trees had a range of direct facilitative and competitive interactions with species in the rangeland, differentiated primarily by the identity or functional group of the recipient species (Figure 11; Ndhlovu et al. 2016). The

tall stature and thicket formation of the *Prosipis* trees was a novel growth trait in the invaded community, and had a competitive effect by reducing light availability for shrubs and annual grasses (Ndhlovu et al. 2016). On the other hand, shade-tolerant and nutrient-loving functional groups of species (primarily perennial grasses) were facilitated by *Prosipis* invasion and increased in percent cover, as the benefits of nitrogen enrichment outweighed the mainly neutral effect of shading (Ndhlovu et al. 2016). Nitrogen enrichment also directly facilitated the germination and growth of three existing non-native species (Ndhlovu et al. 2016).

Importantly, these direct interactions also generated indirect effects that further reinforced the overall impact of the invader. Reducing light availability for light-starved native species indirectly facilitated the spread of the existing shade-tolerant non-native species (Ndhlovu et al. 2016). In uninvaded areas of the rangeland, the non-native species competed poorly against native vegetation, which maintained a low non-native species cover in the rangeland environment. However, the reduction in native species cover driven by *Prosipis* invasion reduced the competition between existing native and non-native vegetation, indirectly promoting the spread of the non-native species. This served to strengthen the direct effect of the invasional meltdown pathway, and ultimately led to an overall compositional change in the community, with an increase in non-native species cover and a decrease in native species richness (Ndhlovu et al. 2016).

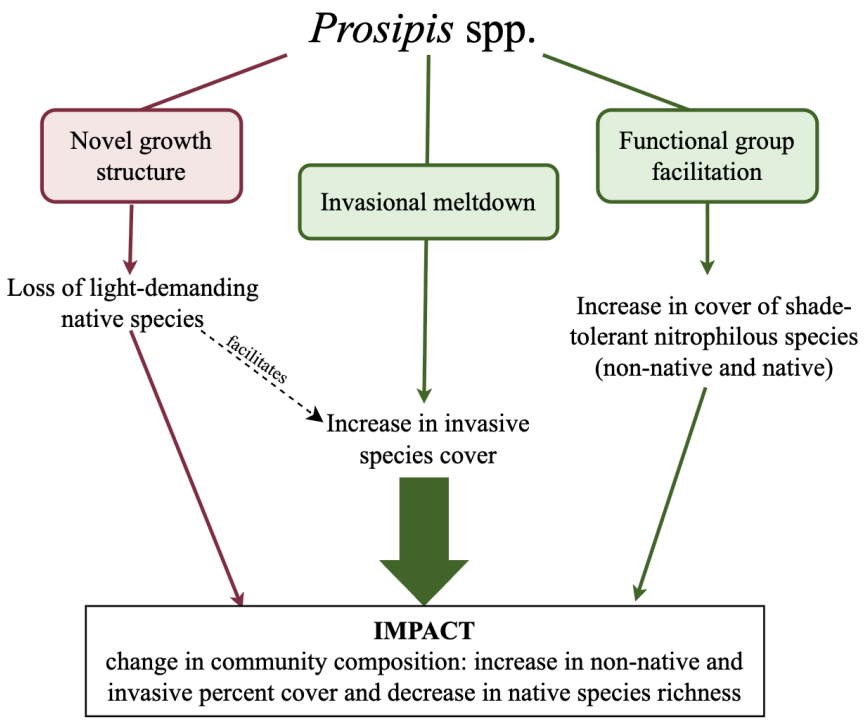

Figure 11: Conceptual diagram of facilitative and competitive interactions, direct and indirect, driven by *Prosipis* trees in South African rangeland environments, and the resulting community impact in terms of biodiversity, density, and composition. Boxes correspond to previously described pathways of competition and facilitation. Solid arrows represent direct effects and dashed arrows represent indirect effects. Thicker arrows represent a stronger effect. All information displayed comes from Ndhlovu et al. (2016).

2. Net facilitation and net competition

While Ndhlovu et al. (2016) provides an excellent example of impacts driven simultaneously by facilitation and competition, it is also common for a particular interaction to dominate in an invaded community. In this case, the

strength of one set of interactions can outweigh that of the other (Muñoz Vallés et al. 2014).

One useful conceptual approach to exploring these two types of interactions is to imagine facilitation and competition as existing on a continuum in a given community (Callaway and Walker 1997; Callaway 2007; Ortiz and Wolf 2024). For example, a community where only competitive or only facilitative interactions occur would exist on one of the two extremes of a continuum (Figure 12). More often than not, the set of interactions in a community exist at some point along the continuum, with varying balances of competitive and facilitative interactions. A community closer to the facilitation end of the continuum would be one where the strength of facilitative interactions outweighs that of the competitive interactions (Figure 12; Muñoz Vallés et al. 2014).

Figure 12: Continuum of facilitation and competition in plant communities.

As such, ecologists often classify plant–plant interactions in a community as having a net facilitative or net competitive effect, determined by the relative strength of the interactions (Callaway 2007; Muñoz Vallés et al. 2014). The dominant set of interactions would then drive the impact on community composition and dynamics (Maestre et al. 2005; Callaway 2007). Therefore, identifying the dominant interaction in a community can be very useful in predicting how that community is structured.

In order to identify the net effect of plant–plant interactions in a community, it is useful to identify the factors that control the strength of facilitation and competition relative to one another in the invaded communities. Understanding these factors gets at a fundamental question: if invasive N-fixing plants are capable of both competitive and facilitative interactions, why does the occurrence of these interactions sometimes differ across environments and between species? The factors outlined below were common across the examined literature for this review.

2.1 Environmental conditions

The stress-gradient hypothesis (SGH) is a well-documented explanation for the varying dominance of facilitative and competitive interactions (Bertness and Callaway 1994; Von Holle 2013). The SGH proposed that the frequency of positive interactions increases with abiotic stress, while competitive interactions are more common in lower stress environments (Bertness and Callaway 1994).

This theory has been supported by several studies on invasive N-fixing legumes (Van Riper and Larson 2009; Werner et al. 2010). For example, Werner et al. (2010) conducted a greenhouse experiment in which the invasive legume *Acacia longifolia* was grown with two native species under high water and drought conditions. Under the high stress drought condition, there was a positive interaction between the study species, while there were strong competitive effects between the species in the well-watered condition (Werner et al. 2010).

Some findings are contrary to the SGH (Ortiz and Wolf 2024). Competitive interactions by invasive N-fixers have outweighed facilitation in some resource-poor environments, despite the fact that those environments would be considered more stressful (Esquivas et al. 2015; Garrett and Gibson 2020). This is primarily true when the limiting resource is something other than nitrogen, and the N-fixer has a high uptake rate of that resource (Esquivas et al. 2015; Garrett and Gibson 2020; Ortiz and Wolf 2024). Esquivas et al. (2015) found that the positive effects of stress amelioration by the N-fixer *Retama monosperma* were outweighed by the negative effects of high water uptake, in part because water was the limiting resource in the system. Researchers have also found instances where interactions between an N-fixer and surrounding species shifted from net negative to net positive as water availability increased, because the species were no longer competing for limited water in the system (Zhang et al. 2018).

The line between condition and resource becomes a little blurry with the SGH. Although the hypothesis is framed in terms of abiotic stress (conditions), many key stressors for plants—particularly water—are limiting resources (Bertness and Callaway 1994). In this sense, resource limitation can function as a form of abiotic stress. This overlap helps explain why many examples of the SGH in systems with invasive N-fixing species involve drought and water uptake, where shifts in interaction type reflect both stress amelioration and competition for a limiting resource.

Alternatively, environmental conditions such as soil texture have been shown to mediate the balance of facilitation and competition for invasive N-fixing plants (Ortiz and Wolf 2024). Ortiz and Wolf (2024) conducted a meta-analysis on both invasive and native N-fixers, and found that facilitation was more common in loamy and loamy-sand soils while competition was more common in sandy soils. They attributed this difference primarily to the physical and chemical attributes of the soils, specifically because sandy soils have higher rates of nitrogen leaching than loamy soils (Ortiz and Wolf 2024). Soil texture, therefore, can affect nutrient levels and resource availability.

2.2 Density of invasive N-fixer

The literature tends to agree that facilitative interactions are more common at lower densities of the invasive N-fixer, while competitive interactions are more common at high densities (Muñoz Vallés et al. 2014; Meira-Neto et al. 2018;

Hansen et al. 2021). Several studies examined the same invasive N-fixer within the same environment across a range of densities and consistently found a shift from net facilitative effects at low densities to net competitive effects at high densities (Muñoz Vallés et al. 2014; Meira-Neto et al. 2018; Hansen et al. 2021).

This pattern likely reflects increasing limitation of space and light as plant density rises (Grams and Lüttge 2010). At low densities, neighboring plants may benefit from localized nutrient enrichment or habitat modification by the N-fixer. However, as density increases, these benefits are increasingly offset by crowding, shading, and displacement, reducing the likelihood of positive interactions.

In many systems, increasing density over time is itself a consequence of nitrogen fixation. In low-nutrient environments, plant density is often constrained by resource availability (Funk 2013). By increasing nitrogen availability, invasive N-fixers can facilitate their own population growth, ultimately creating the high-densities under which competitive effects become more pronounced.

Plants do not necessarily have a homogeneous density across an environment, meaning that density of an N-fixer can explain some of the spatial variation in facilitation and competition (Dickie et al. 2005). Walker and Chapin (1987) found that the actinorhizal N-fixer *Alnus incana* inhibited plant growth when multiple plants grew together, primarily because of their thicket-forming tendencies. However, isolated *A. incana* outside of the patches of dense thickets had an overall positive effect on the neighboring vegetation (Walker and Chapin

1987). This highlights how local density can mediate whether invasive N-fixers act as facilitators or competitors within the same system.

2.3 Life stage of interacting species

The life stage of the invasive N-fixer or the surrounding vegetation can impact the outcome of interactions (Callaway and Walker 1994). Here, life stage refers to developmental phases such as seed, seedling, juvenile, and reproductive adult, and reflects both the time a plant has been established at a site and its growth rate (Callaway and Walker 1994).

An invasive N-fixer may have differing facilitative or competitive effects depending on the life stage of neighboring species, but over the lifetime of a neighboring species there may be a net positive effect (Morris and Wood 1989; Walker and Vitousek 1991; Georgen and Chambers 2012). Walker and Vitousek (1991) found that litterfall from the invasive N-fixing tree *Myrica faya* reduced the germination of a native plant's seedlings. However, the nutrient enrichment from the litterfall had an overall positive effect on the height and biomass of the seedlings that did manage to germinate, and those seedlings did better than the ones that were not growing below *M. faya*. Similar patterns have been observed in studies of native N-fixers, where early life-stage inhibition was coupled with later facilitative effects driven by nutrient enrichment (Morris and Wood 1989; Georgen and Chambers 2012).

In other cases, the effect of the invasive N-fixer may shift at different stages of its own life cycle. Stinca et al. (2015) found that the facilitative effects of the invasive legume *Genista aetnensis* (Biv.) DC. on neighboring plant species were size- and age-dependent, with non-significant effects from seedlings and juveniles, and significant facilitative impacts from large adult plants. This was largely because the large canopy of adult plants mitigated high temperatures and soil water loss to the benefit of species growing below the canopy, while the juvenile plants were not large enough to create such habitat modifications (Stinca et al. 2015). The older plants also produced higher quantities of litter, substantially increasing the availability of inorganic nitrogen compared to juvenile plants (Stinca et al. 2015). In other cases, the quantity of nitrogen added to the soil varied on a seasonal basis. For example, when an N-fixing plant is flowering, it contributes more energy towards reproductive organ growth, reducing the quantity of nitrogen fixed (Watt et al. 2003).

These life-cycle and life-stage differences alter the quantity and timing of nitrogen inputs to the soil, which contributes to temporal variation in facilitation and some lag in the effects of N-fixing invaders. Slower-growing N-fixers may require longer periods to accumulate nitrogen in their tissues and subsequently contribute it to soil nutrient pools (Van Riper and Larson 2009). This delay between establishment and detectable impacts on nutrient cycling is often referred to as a lag effect, and it may result in facilitative interactions emerging only after substantial time has passed (Van Riper and Larson 2009; Ortiz and Wolf 2024).

2.4 Recipient community composition

Both facilitation and competition can be species- or functional group–specific (Gavilán et al. 2016; Ndhlovu et al. 2016; Fill et al. 2019). Facilitative effects may be unevenly distributed because certain species or functional groups respond more strongly to soil nitrogen enrichment than others (Fill et al. 2019). On the other hand, competitive interactions often depend on the degree of niche overlap, particularly whether co-occurring species rely on the same limiting resources as the invasive N-fixer (Marchetti et al. 2023). If a system is dominated by a particular functional group or species, then the impact of the N-fixer may skew towards whatever interaction it has with that dominant group.

Garrett and Gibson (2020) provide an excellent example of this. In the system it invades, the invasive N-fixer *Lespedeza cuneata* facilitates grass species while simultaneously competing with forbs and other legumes (Garrett and Gibson 2020). Because the invaded community was dominated by forbs and legumes and contained relatively few grasses, the net effect of *L. cuneata* at the community level was competitive (Garrett and Gibson 2020).

TEMPORAL DYNAMICS

Biological invasions are processes that unfold over time (Marchetti et al. 2023), and both the nature of their impacts and the relative strength of interaction types can shift as invasions progress. Because invaded systems are themselves dynamic, the interactions that structure plant communities—particularly competition and facilitation—are also expected to change through time (Callaway 2007). Additionally, the factors mediating these interactions, including environmental conditions, density of the N-fixing invader, life stage, and recipient community composition, are not static and often vary across invasion stages or successional trajectories (Strayer et al. 2006). Incorporating time, whether as time since invasion or successional stage, is therefore essential for understanding invasion impacts.

However, incorporating temporal dynamics into impact synthesis can be difficult. Studies on invasion impacts conducted over long periods of time are rare, in part because grant-funded research is not always conducive to long-term studies (Strayer et al. 2006). This limitation is reflected in the literature reviewed here, which is dominated by short-term studies, many conducted within a single year (Table 4). Because of this, the long-term impacts of invaders are often inferred rather than directly tested (Strayer et al. 2006). In this section, I aim to cover several approaches to inferring temporal dynamics of invasions by N-fixing plants from a mechanistic standpoint, by focusing on how the balance of

facilitative and competitive pathways shifts over time and how impacts by invasive N-fixing species interact with successional trajectories.

1. Shifting balance of pathways over invasion stages: Meira-Neto et al. 2018 case study

One way to approach the temporal dynamics of invasion impacts in the context of this review is to identify the multiple facilitative and competitive pathways present in a system and consider how their relative strengths might shift as invasion progresses. If we know the pathways and the factors controlling their strength, we are in a better position to infer how impacts in invaded systems might evolve over time. For example, interactions that appear weak or negligible at the time of study may become more important as environmental conditions or species densities shift (Holmgreen et al. 1997; Dickie et al. 2005; Maestre et al. 2005).

The study conducted by Meira-Neto et al. (2018) illustrates how facilitative and competitive interactions may coexist during early stages of invasion. It also demonstrates how identifying multiple interaction pathways can help generate hypotheses about how invasion impacts may change over time.

This study was conducted at an early phase of invasion by the leguminous tree *Acacia mangium* in nutrient-limited Brazilian white sand grasslands (Meira-Neto et al. 2018). The findings at this stage of invasion were relatively

simple. *A. mangium* had a net facilitative effect on neighboring plants, and invaded plots were associated with an increase in total species richness (Figure 13; Meira-Neto et al. 2018). Facilitation was conducted primarily through soil nitrogen enrichment and some direct nitrogen transference, as evidenced by increases in soil nitrogen and leaf $\delta^{15}N$ values (Meira-Neto et al. 2018).

However, the researchers also identified interaction pathways that could potentially become competitive as invasion progresses. In the open grasslands studied, uninvaded areas were characterized by high light availability and sparse canopy cover. Even at relatively low density, *A. mangium* introduced a novel growth structure to the system by forming a denser canopy than most native species, reducing light availability beneath the trees (Figure 13). At the time of data collection, this shading effect did not appear to have strong competitive consequences for neighboring plants. Increased nitrogen availability was also associated with higher specific leaf area in neighboring plants, which could further increase shading in invaded stands. In addition, *A. mangium* showed evidence of self-facilitation, as its own seedlings appeared to benefit the most from both shaded conditions and elevated soil nitrogen levels (Meira-Neto et al. 2018).

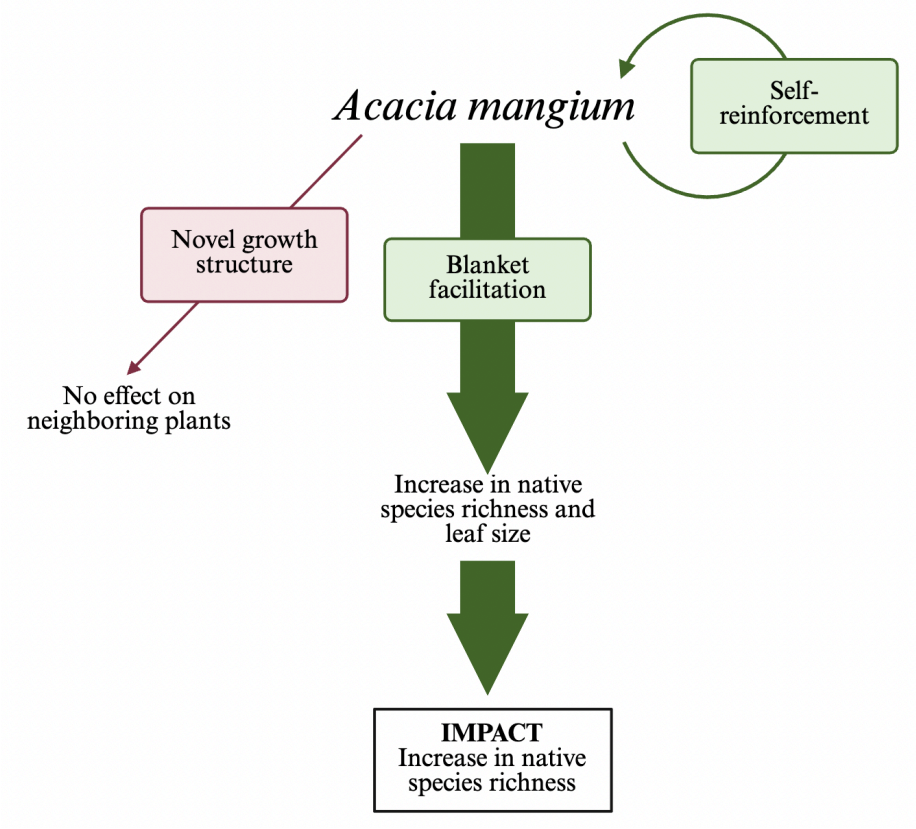

Figure 13: Conceptual diagram illustrating observed facilitative and competitive interactions driven by *Acacia mangium* trees during early invasion in Brazilian white sand grasslands, and the resulting community impact in terms of biodiversity, density, and/or composition. Red boxes and arrows indicate previously described competitive pathways, while green boxes and arrows indicate facilitative pathways. Solid arrows represent direct effects, and thicker arrows denote stronger effects. All information is derived from Meira-Neto et al. (2018).

Because the study captured an early stage of invasion, these observations allowed the researchers in the study to generate hypotheses about how interactions may change as the invasion progresses. From a mechanistic perspective, these dynamics can be understood as changes in the relative strength of different pathways through time. Facilitative interactions associated with

nitrogen enrichment may initially dominate the system, increasing species richness. As invader density increases and canopy cover expands, however, competitive interactions may become more important.

For example, self-facilitation by *A. mangium* has the potential to become a positive feedback cycle, leading to increasing dominance of the invader in the system (Wilson and Agnew 1992; Callaway 2007; Meira-Neto et al. 2018). Increasing dominance, coupled with the dense canopy of the invader and increasing leaf area of facilitated species, has the potential to fundamentally alter light availability in the system (Meira-Neto et al. 2018). This would have consequences for the growth and survival of the many native light-demanding species in the grassland (Meira-Neto et al. 2018). Here, light-demanding refers to species that require direct, abundant sunlight for growth and reproduction, meaning they fare worse in the shade than their competitors (Marchetti et al. 2023).

Figure 14 illustrates how increasing the strength of the self-facilitation interaction can indicate the transition to a positive feedback loop. Assuming that the density of the N-fixer increases, the strength of the blanket facilitative interaction might decrease and be overcome by a competitive novel growth structure pathway. Because the N-fixer is taller than other species in the system, it will have disproportionate effects on the light-dependent native species. That effect coupled with further shading from neighboring plants may lead to steep declines in the native species in later invasion stages.

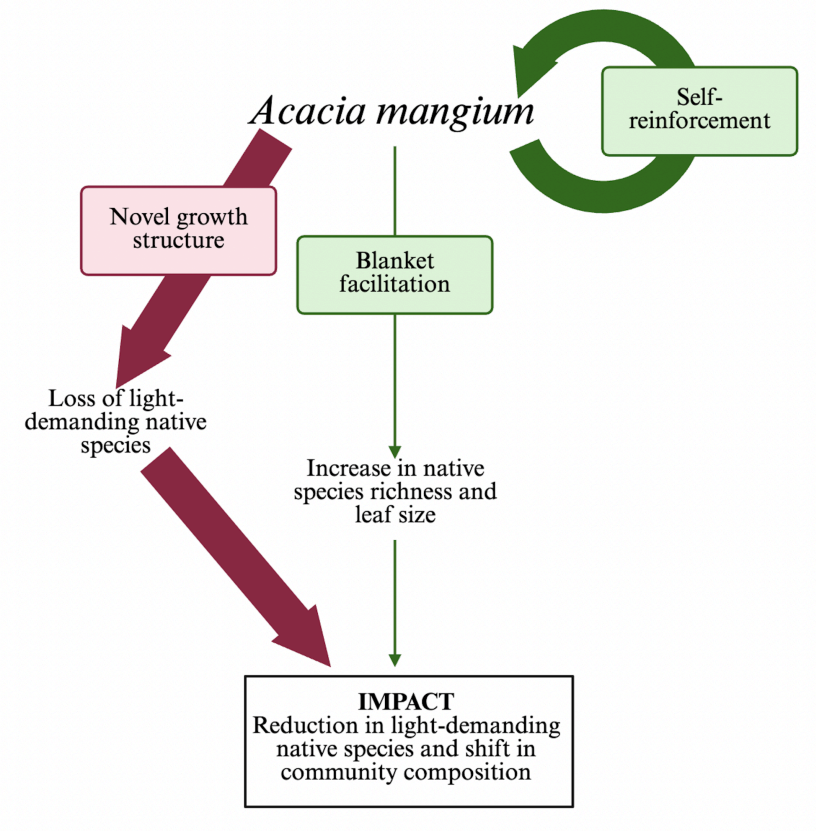

Figure 14: Conceptual diagram illustrating hypothesized facilitative and competitive interactions driven by *Acacia mangium* trees during later invasion in Brazilian white sand grasslands, and the resulting community impact in terms of biodiversity, density, and/or composition. Red boxes and arrows indicate previously described competitive pathways, while green boxes and arrows indicate facilitative pathways. Solid arrows represent direct effects, and thicker arrows denote stronger effects. All information is derived from hypotheses by Meira-Neto et al. (2018).

By identifying both facilitative and potentially competitive interactions, studies such as Meira-Neto et al. (2018) illustrate how mechanistic pathways can be used to generate hypotheses about how invasion impacts may evolve through time. Understanding these shifts is important not only for predicting how invasion impacts may develop within a particular system, but also for considering how

such mechanisms interact with the broader processes that govern community change, including ecological succession.

2. Succession as a perspective for pathways over time

Up until this point, I have positioned the impacts of invasive N-fixing species as changes to community dynamics. Yet, change is a central part of plant communities in the long term, regardless of the presence of an invasive species (Marchetti et al. 2023). This presents a challenge in attempting to predict long-term outcomes, specifically distinguishing between natural change in a community—or succession—and an altered state induced by invasion of an N-fixing species. Succession refers to the predictable series of changes in a plant community over time progressing from a barren environment with no organic matter (primary succession after post-glaciation or volcanic destruction) to a climax community (Marchetti et al. 2023). Most succession that we observe is secondary succession, typically beginning following a disturbance (Marchetti et al. 2023). Each sequence of changes to the plant community is called a sere, and transition to the next sere involves a change in the dominant plant species (Marchetti et al. 2023). Early successional seres have very low nutrient availability and very few species, and one of the primary drivers of succession is the accumulation of organic matter and nutrients, particularly nitrogen (Walker and Syers 1976).

Not surprisingly, early succession and the colonization and population growth of N-fixing plants are often interconnected. Native N-fixing plants frequently act as pioneer species in early successional environments, meaning they add nitrogen and organic matter and help to build soil (Chapin et al. 1994). Colonization of disturbed, low-nutrient soils by these plants gradually enriches the substrate with nitrogen, creating more favorable growing conditions for late-successional species (Connell and Slatyer 1977). Invasive N-fixing species may similarly drive successional change (Scherer-Lorenzen et al. 2007). However, the tendency for invasive N-fixers to modify habitats by virtue of invading low-nutrient systems means that they also have the potential to alter successional trajectories.

Disentangling impacts and successional processes is far beyond the means of this review. Instead, succession can provide a useful framework for approaching the long-term impacts of invasive N-fixing plants. Rather than viewing invasion impacts as isolated changes to biodiversity or density, they can be understood as reinforcing or modifying the processes that govern community turnover over time. Understanding how these short term impacts may interact with successional processes can be a useful way of considering what information we can suggest about long-term outcomes. Specifically, I suggest that it may be useful to approach long-term impacts by examining the extent to which an invasive N-fixing species influences or alters succession in the invaded community (David et al. 2015). Do these short-term changes seem to be in line

with the changes to community structure that we expect with succession or do they seem to be unpredictable and directing the community towards a different course?

To be clear, these are purely theoretical trajectories over time based on findings from the literature and ecological theory. They are by no means predictions, and cannot currently be applied to the examples in the literature. Additionally, these trajectories are distinguished by the extent to which an invasive N-fixing species modifies a community or ecosystem. Without a measure of impact magnitude, I can only distinguish between these trajectories on a theoretical basis. While the concepts below are based on findings from the experimental literature, I do not make any attempt to sort the literature into the different trajectories. They are only used to guide my thinking.

2.1 Inducing, accelerating, or inhibiting succession.

Invasion by an N-fixing plant may induce, accelerate, or inhibit transitions between successional stages. In these cases, the invasive N-fixer alters the rate at which succession occurs, but does not necessarily cause the community to diverge from its expected successional trajectory. Instead, the community may still progress through succession in a predictable way for that ecosystem type, though the timing and mechanisms of these transitions may differ from those observed in uninvaded systems.

Positive interactions by invasive N-fixing species may act in accordance with the facilitation model of succession, which suggests that early-successional species modify the environment so that it is more favorable for late-successional species (Connell and Slatyer 1977). In primary successional environments, invasions by N-fixing species can induce or accelerate succession (Vitousek and Walker 1989). By rapidly altering resource availability, invasive N-fixers can shorten the time required for later-successional species to establish. Prior to the invasion of the legume *Lupinus nootkatensis*, alpine woodland and grassland systems in southeast Iceland consisted primarily of early-successional species adapted to low-nutrient conditions (Vetter et al. 2018). Because these systems occur in a cold biome, natural successional processes tend to proceed very slowly (Vetter et al. 2018; Prach and Walker 2020). Climate warming in the region expanded the suitable habitat for *L. nootkatensis*, facilitating its invasion into these colder environments. Following invasion, *L. nootkatensis* rapidly increased nitrogen cycling in the nutrient-poor soils through litter decomposition, which in turn facilitated the establishment of native nitrophilous ruderal species (Vetter et al. 2018). These species represented a later successional stage relative to the existing vegetation, suggesting that the invasion accelerated the progression of the community toward a later successional state. That said, the facilitated native species were consistent with the type of vegetation ecologists would expect to see at later successional stages in that particular environment, meaning that invasion by *L. nootkatensis* did not alter the typical successional trajectory. In this case,

invasion simply triggered a rapid onset of successional change in a system where succession would otherwise occur very slowly (Vetter et al. 2018; Prach and Walker 2020).

Alternatively, competitive interactions by invasive N-fixers may fit within the inhibition model of succession (Connell and Slatyer 1977). In the inhibition model, species compete with and inhibit the establishment and growth of later successional species (Connell and Slatyer 1977; Marchetti et al. 2023). The latter only colonize the system after the first species is damaged or killed, opening up resources and transitioning the system to the next successional sere (Connell and Slatyer 1977). Where facilitation is common in early successional environments, inhibition is more common in later successional seres (Marchetti et al. 2023). If an N-fixing species invades and successfully outcompetes native species, either through novel growth traits or resource use, its subsequent dominance may act as an inhibiting force in the successional trajectory (Gusev 2019). Whether this ultimately alters the long-term successional trajectory depends on what occurs after the dominance of the N-fixer declines. If subsequent disturbance allows native species to reestablish, the community may continue along its expected successional pathway (Connell and Slatyer 1977). However, if the death or removal of the N-fixer instead facilitates the establishment of other invasive species, the community may shift toward a novel trajectory, which I will cover in the next section.

Studies of ecosystem restoration following invasion by N-fixing plants provide some insight into these possibilities, as they allow researchers to examine community responses after the dominance of the invader is reduced or removed. Pickart et al. (1998) examined the effect of removing the dominant invasive N-fixing species *Lupinus arboreus* from dune ecosystems. After four years, the cover of native species had increased again in the previously invaded patches (Pickart et al. 1998). This suggests that, once the inhibiting force of the invader was removed, the community was able to return to what would be considered a typical composition (Pickart et al. 1998).

In the context of invasive N-fixing species, processes that accelerate succession and those that inhibit it may not be mutually exclusive. Instead, they may occur at different stages of community development or of invasion. In the facilitation model of succession, early-successional species are gradually replaced by later-successional species over time (Connell and Slatyer 1977; Marchetti et al. 2023). However, if an invasive N-fixer is both a strong facilitator and a strong competitor, it may initially promote the establishment of other species while later preventing their replacement. In systems invaded by N-fixers, early facilitative interactions may therefore accelerate the establishment of additional species and increase overall biomass. However, as space and other resources become limiting, interactions may become increasingly competitive (Muñoz Vallés et al. 2014; Meira-Neto et al. 2018; Hansen et al. 2021). If the invasive N-fixer is a superior competitor under these conditions, its dominance may inhibit further successional

change. In this way, facilitation-driven acceleration of succession may eventually give way to competitive inhibition as community density shifts over time.

2.2 Altering successional trajectory

Invasive N-fixing plants that substantially modify an invaded ecosystem may be in a position to redirect the successional trajectory of a community entirely (Vitousek and Walker 1989; Hughes and Denslow 2005). In this case, invasion by an N-fixer may tip the community in a successional direction that results in a different community type than would typically be expected. Species that engage in what we might consider novel ecosystem construction can go beyond just increasing or decreasing the rate at which succession occurs.

But what exactly does it mean to alter the direction of succession? When ecologists examine this in the context of community dynamics, this redirection of succession can culminate in what is termed an alternative stable state (Hobbs and Sudding 2008). An alternative stable state is a novel equilibrium community characterized by structure and function that differ from the typical community expected for a system (Hobbs and Suding 2008). We can think of equilibrium states as potential endpoints for succession (Marchetti et al. 2023). The transition to an alternative stable state occurs when a significant enough disturbance provides momentum to shift the community composition out of its current stable state and towards a different one with different species composition (Marchetti et al. 2023).

The transition between stable states is often described as a regime shift, referring to a rapid transition in which a system crosses a threshold and begins moving toward a different equilibrium state (Scheffer et al. 2001). Once the system crosses this threshold—sometimes referred to as a tipping point—it is nearly impossible to return the community to its original equilibrium state without changing fundamental processes and disturbances associated with the ecosystem (Scheffer et al. 2001). Regime shifts typically arise from positive feedbacks within ecosystems that reinforce particular community compositions or disturbance regimes, and drive substantial changes in ecosystem functioning (Scheffer and Carpenter 2003).

Invasion by an N-fixing species may alter the structure and functioning of a community in ways that trigger such a regime shift. In the context of the plant–plant interactions discussed in this review, invasional meltdown is the most likely pathway to contribute to these feedbacks. If an invasive N-fixer facilitates another invader that further alters nutrient cycling or disturbance regimes, the combined effects can create reinforcing feedbacks that push the system beyond a threshold (Archer et al. 1995; Adler et al. 1998; Dornbusch et al. 2018). The invasional meltdown described by Adler et al. (1998), in which the N-fixer *Myrica faya* facilitated invasive grasses, provides a clear example. These grasses increased the frequency and intensity of fire, generating a positive feedback that reinforced their own dominance (D'Antonio and Vitousek 1992; Adler et al.

1998). Such shifts in disturbance regimes are well known to drive transitions to alternative stable states (Scheffer et al. 2001).

Such a drastic change to an ecosystem is rarely only driven by plant–plant interactions, or the pathways covered in this paper. Clearly, the species must have ecosystem-wide impacts. The species in the dataset that are described as altering successional trajectories are also often described as ecosystem engineers or ecosystem transformers (Archer et al. 1995; Richardson et al. 2000; Vetter et al. 2018). By altering both community composition and ecosystem functioning, these species can be described as constructing novel ecosystems (Hobbs et al. 2006; Vetter-König 2024).

While not explicitly described as an example of a shift to an alternative stable state, Hughes and Denslow (2005) provides an excellent example of how invasion alters the structure and function of a community over different successional stages. The study was conducted using a chronosequence, which is a method of studying long-term ecological change by comparing similar sites at different ages (Marchetti et al. 2023). Over three chronosequences, representing 48, 213, and 300 year old lava flows, the invasive N-fixing tree *Falcataria moluccana* shifted the community composition from entirely native species-dominated to invasive dominated (Hughes and Denslow 2005). This was directly attributed to the substantial increase in nutrient cycling in invaded stands. This alteration to the functioning of the ecosystem preferentially facilitated the establishment of invasive species, in an example of invasional meltdown. The

heavily invasive-dominated community at the later successional stage (300 year old lava flow) indicated that *F. moluccana* shifted the long-term trajectory of community composition (Hughes and Denslow 2005).

Therefore, distinguishing between changes in the rate of succession and changes in successional trajectory requires understanding the magnitude of ecosystem modification caused by the invader. If invasion primarily alters interactions among species without fundamentally changing ecosystem processes, it may simply accelerate or inhibit succession along an existing trajectory. However, when an invasive N-fixer substantially alters ecosystem functioning, particularly through ecosystem engineering, it may push the community toward an entirely different successional endpoint (Richardson et al. 2000).

LIMITATIONS

The limitations of this study fall into two distinct categories: limitations within the selected studies, which restricted synthesis, and limitations related to the scope and conceptual simplifications required for this project.

1. Limitations in the literature

1.1 Inconsistent measure of impact

The initial aim of this review was to examine how invasion by N-fixing plants manifests in changes to biodiversity, community density, and community composition. At least one measure of these parameters was required for inclusion in the literature search. However, the studies included in this review used inconsistent methods for measuring these variables, which made qualitative synthesis difficult.

Across the studies examined, biodiversity was quantified using several different metrics, including species richness, the Shannon–Wiener index, and measures of functional diversity. Density was most often measured using biomass, although some studies instead used percent cover. Community composition was rarely explicitly quantified; only 24% of the reviewed studies included a measure of compositional change.

Although these metrics broadly capture aspects of biodiversity or community density, they measure different components of community structure.

Reconciling these differences was beyond the scope of this review and limited the ability to synthesize impacts across studies. Additionally, some studies distinguished between native and non-native species or between functional groups when reporting biodiversity and density metrics, whereas others reported only total community values. This inconsistency further complicated comparisons among studies.

1.2 Time scale

The methodology of the reviewed studies made it difficult to incorporate time as a variable in my approach to impact synthesis. Data collection for a majority (80%) of the studies was conducted in a year or less, and of those studies, 56% were based on data collected at only one point in time (Table 4). This meant that temporal variation in plant–plant interactions or in community impacts was not captured in most of the studies. Additionally, most studies either did not or were unable to explicitly state the time since invasion by the N-fixing species in that particular system. This made it difficult to place the interactions occurring at the time of the study into the temporal context of the invasion, which limited the ability to map changes in interactions over the course of an invasion (Strayer et al. 2006).

1.3 Mechanisms

The studies included in this review differed in the extent to which they tested the mechanisms underlying invasion impacts (Table 4). Some studies were purely observational, comparing biodiversity or community composition between invaded and uninvaded sites. In these cases, mechanisms were inferred by the authors rather than directly tested. Other studies explicitly tested mechanisms through experimental manipulation. Both types of studies were included in this review because even inferred mechanisms can provide insight into the processes underlying community change.

However, the reliance on inferred mechanisms may reduce confidence in some of the conclusions drawn in this review. As Didham et al. (2005) argued, this kind of approach opens up the possibility that the invasive species itself is not the driver of the community change. Rather, it could be that the disturbance driving community change and native species loss comes from elsewhere, for example habitat fragmentation or warming climate. The invasive species may instead simply be a byproduct of that disturbance, and not the driving force. While I hesitate to say that is true for all invasive N-fixing plants, a better test of causal mechanisms would push against that argument (Ortiz and Wolf 2024). This limitation reflects a broader pattern in invasion ecology. Many studies of invasive species impacts focus on documenting ecological change rather than experimentally testing the processes responsible for those changes (Levine et al. 2003).

1.4 Taxonomic and geographic bias

The studies included in this review were not evenly distributed across genera or geographic regions. Many focused on similar genera of invasive N-fixing plants, with *Acacia*, *Lupinus*, and *Lespedeza* overrepresented in the pool of experimental papers (Table 2). The most common genera in this study correspond to some of the more highly-studied species within invasion ecology (Scherer-Lorenzen et al. 2007). Invasion ecology research on N-fixing plants also tends to focus disproportionately on woody species (Chiu et al. 2023), which was also represented in the dataset for this review (Table 2). Geographically, a large portion of the studies in this review were conducted in North America and Europe (Figure 1). This reflects some of the bias in invasion ecology research, with a disproportionate number of studies conducted in regions of North America and Europe, Australia, and New Zealand (Chiu et al. 2023). As a result, the patterns identified in this review may reflect interactions occurring within a limited subset of ecosystems and species.

1.5 Inconsistent reporting of contextual variables

Certain contextual information could not be used for synthesis in this review, simply because the papers did not consistently report that information. Some examples of variables that were inconsistently reported include: successional stage of the invaded system, status of nutrient availability in the system, density of the invasive N-fixer, and composition of the recipient

community. This review and future syntheses of papers on N-fixing invaders would benefit from a consistent set of reported contextual variables.

2. Limitations of the review

The goal of this review was to produce a generalized mechanistic approach to the processes underlying community impacts of invasions by N-fixing plants. Ecological interactions and impacts of invasive N-fixing plants are by nature incredibly complex. Therefore, to be able to produce some synthesis across the papers with a variety of species and ecosystems, I had to make some assumptions and smooth over some complexities. For that reason, the findings I have produced in this paper should be approached as a cartoon, in the sense that they provide a simplified representation of the interactions occurring, but lack some of the complexity of these real world impacts. Below, I will outline the topics that were either left out of the review or generalized to keep a reasonable scope for the paper.

2.1 Variation in magnitude of nitrogen enrichment

One of the primary limitations of this review surrounds the minimal focus on variation in the magnitude of nitrogen enrichment from invasive N-systems. I treated nitrogen enrichment as a relatively uniform driver of ecological change in this review. I did not account for the immense variation in magnitude of soil

nitrogen addition when creating my pathways, beyond simply stating that the interactions were mediated by nitrogen enrichment. Therefore, this review did not incorporate a synthesis of the variation in nitrogen enrichment, and how that might influence the strength of particular interactions and the impact overall.

My ability to account for this variation was limited by the qualitative nature of the review, as well as my own limited expertise on the subject. As with impact synthesis, comparing nitrogen enrichment across studies was difficult without a method of quantitative analysis. The studies examined differed in how nitrogen enrichment was measured; some directly quantified soil nitrogen content, while others used indirect indicators such as leaf $\delta^{15}N$ to infer uptake of fixed nitrogen (Hellmann et al. 2011; Lorenzo et al. 2017; Boscutti et al. 2020). Integrating these different metrics to compare the magnitude of nitrogen enrichment across systems was not feasible within the scope of this review.

In reality, invasive N-fixing species vary widely in their contributions to soil nitrogen, both among species and across environments. Rates of nitrogen fixation are influenced by the presence of rhizobial bacteria and environmental conditions, particularly existing soil nitrogen and phosphorus availability (Scherer-Lorenzen et al. 2007; Vitousek et al. 2013). Additionally, the release of nitrogen through decomposition depends on external factors such as temperature and soil moisture (Conant et al. 2011). Species traits also contribute to this variation: long-lived N-fixers may contribute larger total inputs of nitrogen over time, while shorter-lived species may provide more continuous inputs. Similarly,

woody and non-woody N-fixers differ in how nitrogen enters the system, with woody species often associated with fewer, larger inputs and non-woody species contributing more consistent additions (Ehrenfeld 2003; Ortiz and Wolf 2024).

Given that nitrogen enrichment mediates the interactions described in this review, it is likely that the strength of a given interaction, and the magnitude of its impact, are influenced by the quantity of nitrogen added to the system. Incorporating this variation represents an important direction for future work.

2.2 The role of non-plant mediators in these interactions

This review focuses on plant–plant interactions as the primary drivers of community change, but many impacts of invasive N-fixers are mediated indirectly through non-plant components of the ecosystem. Most importantly, the availability of nitrogen itself—and therefore the interactions described throughout this review—depends heavily on soil conditions and soil microbial communities. Other non-plant mediators, including herbivores and broader trophic interactions, can further alter how these impacts are expressed within plant communities.

Soil microbial communities are especially central to the impacts of invasive N-fixing species. Nitrogen fixation cannot occur without the presence of compatible rhizobial or actinomycete bacteria, meaning that the composition of the soil microbial community plays an essential role in determining whether an invasive N-fixer is able to establish, fix nitrogen, and alter nitrogen cycling in the first place (Hughes et al. 2025). In this sense, many of the plant–plant interactions

described in this review are fundamentally mediated by belowground biotic processes. Variation in microbial community composition may therefore strongly influence both the amount of nitrogen made available in the soil and the extent to which subsequent competitive or facilitative interactions occur.

More broadly, soil conditions and microbial communities also influence the movement and persistence of nitrogen in the system. Processes such as mineralization, decomposition, and microbial immobilization determine how quickly fixed nitrogen enters plant-available pools and how long it remains available to neighboring species (Osman 2013; Weil and Brady 2017). As a result, changes in nitrogen availability cannot be fully understood independently of belowground community dynamics.

By excluding these pathways, this review does not capture the full range of interactions through which invasive N-fixers influence plant communities. As a result, some impacts attributed to direct plant–plant interactions may, in reality, be mediated through multi-trophic processes.

2.3 Role of spatial scale

A major limitation of this review is the lack of explicit consideration of how spatial scale contributes to variation in invasion impacts. This review did not account for the influence of spatial scale of a study—local patch-specific studies versus large-scale landscape-wide studies—when grouping interaction types into pathways.

The spatial scale of an experiment has been shown to influence the detected type and magnitude of community-level invasion impacts (Powell et al. 2011; McMillan et al. 2023). As the spatial scale of analysis increases, environmental heterogeneity, disturbance regimes, and landscape context become more important. Small-scale experiments do not necessarily capture the full range of ecological heterogeneity that likely drives species dynamics across large landscapes (McMillan et al. 2023). This can alter both the magnitude and even the direction of observed invasion impacts. Large-scale studies often report an increase or very little change in community richness after invasion (McMillan et al. 2023), while studies carried out at smaller scales frequently report reductions in biodiversity following invasion (Ricciardi et al. 2013; Yang and Bao 2022).

Spatial scale also influences the balance of facilitative and competitive interactions. This is in part because nitrogen enrichment can be spatially heterogeneous in an invaded system, especially if the N-fixers form patches of nutrient enriched soil (Ehrenfeld 2003). Within a single system, facilitation and competition may have different spatial distributions (Hellmann et al. 2016). For example, competitive interactions may happen primarily below the canopy of the invasive N-fixer, while facilitative interactions happen just outside the canopy where uptake of increased soil nitrogen from the N-fixer is not impeded by competition and shading from the plant (Hellmann et al. 2016). This means that, at a small spatial scale, one interaction may dominate. For example, competitive interactions typically dominate at small scales (Powell et al. 2011). But as the

scale increases, the variation in impacts increases, meaning that that interaction may no longer be dominating the system.

It was difficult to account for spatial scale in this review. Many studies did not state the spatial extent of the study qualitatively, and calculating the spatial scale using plot and site dimensions across different experiments would have required quantitative analysis that was beyond the qualitative focus of this project.

This means that by synthesizing findings across studies conducted at different spatial scales without explicitly accounting for these differences, this review may overrepresent certain interaction pathways based on the dominant spatial scales of the included studies, which may potentially skew the conclusions. The studies included in this review span a range of spatial scales, but based on my brief qualitative analysis, most are conducted at relatively small scales, such as patch-level experiments or localized field surveys. This is typical of most studies in invasion ecology on invasion impacts on community biodiversity (Peng et al. 2019).

2.4 Variation across biomes

Finally, I did not explicitly examine how invasion impacts may differ across biomes. While I considered environmental factors influencing invasion impacts and common ecological conditions across studies, I did not synthesize impacts at the biome level. Environmental conditions such as climate, soil type, and background nutrient limitation vary widely among ecosystems and may

influence both nitrogen fixation rates and plant–plant interactions (Ehrenfeld 2003; Catford et al. 2019). As a result, the mechanisms identified in this review may operate differently across ecological contexts.

This limits the generalizability of the findings presented in the review. The relative importance of the pathways identified in this review can vary among ecosystems, and patterns observed across the literature may be disproportionately influenced by the systems most represented in the pool of literature. In particular, grasslands were overrepresented in the reviewed literature, which may bias conclusions toward the types of interactions and impacts most common in those systems (Figure 2).

Biome-level variation was not explicitly incorporated in this review because the different ecosystems were not evenly represented across the studies. It would have been difficult to compare impacts across groups with very different sample sizes. Additionally, I found that biome-level distinction was not possible within the time frame of this project.

FUTURE DIRECTIONS

As evidenced in the previous section, there are a number of gaps both in this review and in the literature on the impacts of invasive N-fixing species in general. In this section, I aim to lay out several potential next steps and recommendations for future experimental research. This is by no means a comprehensive list of possible future directions, only several gaps that I believe are especially apparent in this review.

1. Meta-analysis of impacts

The next step in a comprehensive review of community-level impacts by invasive N-fixing species would be an approach to quantifying what the impacts actually are. If we think back to the definition of impact at the community level as a measurable change in the properties of the community driven by invasion of the N-fixing species, then the question that has been left unanswered in this review thus far is: what are those measurable changes? Without quantitative synthesis, it was difficult to identify consistent patterns in the magnitude or direction of community change across studies. However, it is still a very necessary piece of examining impacts, as understanding magnitude of impacts is important in the context of evaluating risk of invaders and informing management (Parker et al. 1999).

Approaching this question, then, would best be done with a meta-analysis. A meta-analysis is a statistical method used to quantitatively combine and analyze

experimental results from many independent studies (Vetter et al. 2013). The benefit of a meta-analysis includes higher statistical power, better precision, and overall an ability to address a broader scope than a single study (Vetter et al. 2013). In the context of invasive N-fixing plants, a meta-analysis could be used to evaluate the type, direction, and magnitude of community impacts associated with invasion (Vilà et al. 2011; Ortiz and Wolf 2024). I do not have the statistical expertise to suggest specific methods for this meta-analysis; however I do have suggestions for the type of information that should be included in the analysis.

Thus, for a meta-analysis to adequately capture the complexity of invasive N-fixer impacts, I suggest that it must incorporate two key components: (1) quantitative measures of changes in community structure and (2) contextual variables that influence the strength and direction of those impacts.

A comprehensive meta-analysis should incorporate multiple dimensions of community structure, so as to capture the range of ways the invader might change a community. These metrics should capture changes in community dynamics associated with invasion rather than static snapshots of community properties. For example, the approach for most of the studies in the pool examined for this project was to compare these measures between invaded and non-invaded sites (Levine et al. 2003).

I also want to emphasize the importance of incorporating community compositional changes and functional diversity into the meta-analysis. While most studies incorporated some measure of biodiversity or density, typically in the

form of species richness and biomass, very few measured changes to community composition or functional diversity. However, both of these metrics have the potential to capture different but important facets of biological invasion impacts. For example, it's possible that the species makeup of a community may change drastically without the total number of species in a community changing significantly (Ndhlovu et al. 2016). In that case, a measure of compositional change would capture the impact, while species richness would not. I will also echo Renault et al. (2022) in arguing that functional diversity indices have the potential to capture the homogenizing effect of biological invasions on communities. The functional trait composition of a community can also have implications for ecosystem functioning, thus potentially being an important metric when considering long-term impacts (Hansen et al. 2021).

The key response variables capturing impacts at the community level are summarized in Table 7.

Table 7: Suggested variables for a meta-analysis that capture community impacts. The table includes variable type, example metrics for synthesis and comparison across studies, justification for inclusion in meta-analysis, and associated references.

Variable category	Example metrics	Rationale	References
Taxonomic biodiversity	Species richness, Shannon-Wiener Biodiversity Index, Simpsons Index	Measures changes in community diversity associated with invasions, useful in distinguishing between facilitative and competitive interactions	Hellmann et al. 2011; Vilà et al. 2011; Ortiz and Wolf 2024

Community density	Biomass, percent cover	Captures changes in plant abundance or density, useful in distinguishing between facilitative and competitive interactions	Vilà et al. 2011; Fill et al. 2019; Ortiz and Wolf 2024
Native vs. non-native species responses	Diversity or density of native vs non-native species	Evaluates whether invasion disproportionately impacts native species	Shaben and Myers 2010; Ndhlovu et al. 2016
Functional diversity	Functional richness, functional evenness, functional identity, divergence and dispersion	Captures species' roles within a community, implications for ecosystem functioning	Vandewalle et al. 2010; Hansen et al. 2021; Renault et al. 2022
Community composition	Beta diversity	Quantifies shifts in species identity or dominance	Lazzarro et al. 2015; Boscutti et al. 2020

Equally important is the incorporation of contextual factors that influence the strength and type of invasion impacts. As demonstrated throughout this review, the balance between facilitation and competition associated with invasive N-fixing plants is highly context-dependent. Without ecological context, the analysis may yield variable or counterintuitive results (Ricciardi et al. 2013). In fact, several meta-analyses of invasive species impacts—not necessarily exclusive to N-fixing plants— have found the results to be idiosyncratic without ecological context (Vilà et al. 2011; Ortiz and Wolf 2024; Staccone et al. 2021). Therefore, Table 8 includes a list of factors that this review has indicated to be important in controlling the strength of facilitative and competitive interactions as variables to include in a meta-analysis for the purpose of contextualizing the analysis.

Table 8: Suggested variables for a meta-analysis that capture ecological context of invasive N-fixer impacts. The table includes variable type, example metrics for synthesis and comparison across studies, justification for inclusion in meta-analysis, and associated references.

Variable category	Example metrics	Rationale	References
Invader abundance	Density or percent cover of invasive N-fixer	Density of the invasive species can moderate the relative strength of facilitation and competition	Muñoz Vallés et al. 2014; Meira-Neto et al. 2018; Hansen et al. 2021
Invader traits	Growth form (woody or herbaceous), stature of invader relative to surrounding vegetation, life stage	Invader traits can determine the quantity of N fixed and potentially the type of interaction driving community change	Marchante et al. 2003; Bonanomi et al. 2011
Nitrogen enrichment by invader	Total soil nitrogen, leaf δ^{15}N, N mass of litter	Has the potential to indicate how much the strength of an impact is related to the quantity of nitrogen fixed	Hughes and Denslow 2005; Castro-Díez et al. 2014
Other habitat modification	Light availability, hydrology, substrate stabilization	Can also influence the type of dominant interaction	Watt et al. 2003; Ortiz and Wolf 2024
Environmental context	Biome, soil texture, climate, type of limiting resource, successional stage	Can influence a variety of factors, including: extent of nutrient enrichment, type of dominant interaction, and type of recipient vegetation	Bertness and Callaway 1994; Castro-Díez et al. 2014; Ortiz and Wolf 2024
Characteristics of recipient community	Biodiversity, density, composition, functional traits	The species present in the recipient community can	Garrett and Gibson 2020; Ren et al. 2023
Study design	Spatial scale, experimental	Helps explain variation among studies and over time	Strayer et al. 2006; McMillan

duration	et al. 2023

However, a meta-analysis is not a perfect solution, and it may face several of the same challenges I encountered in this review. In particular, the large variation in impact metrics used across studies and the inconsistent reporting of contextual variables may limit the scope of quantitative synthesis. For this reason, the variables suggested above should be considered not only as components of a future meta-analysis, but also as recommendations for the types of data that future studies on invasive N-fixing plants should prioritize collecting and reporting.

2. Long-term successional dynamics

A second important direction for future research involves understanding how invasion by N-fixing plants interacts with ecological succession. I proposed several possible ways that invasion by N-fixing species may interact with successional dynamics, ranging from altering the rate of succession to entirely redirecting successional trajectories; however those hypotheses were purely theoretical. Succession as a perspective for approaching long-term impacts of invasive N-fixers is a very valuable avenue for future research, particularly as it relates to management of invasive species over time (Sheley et al. 1996). From a restoration standpoint, invasive N-fixing plants that substantially change the nature of the invaded ecosystem and redirect successional trajectories are the

greater threat (Sheley et al. 2006). Therefore, it would be useful to understand how to distinguish between invaders that have limited long-term impacts and invaders that may fundamentally change the nature of the invaded system. However, more empirical research on disentangling invasion impacts from the natural dynamics of successional change is required to make that distinction.

Addressing this gap will likely require approaches that capture ecological change across longer time scales. Long-term monitoring studies would provide the most direct evidence of how invasion impacts unfold through time, but these are often difficult to implement within the constraints of typical research funding cycles (Vucetich et al. 2020). Instead, I suggest that more studies should be conducted using chronosequences. By comparing sites of different ages or invasion stages, researchers can approximate long-term ecological change and provide insight into how invasive N-fixing species influence successional dynamics. Muñoz Vallés et al. (2011) provides an excellent example of study design that can capture longer-term impacts using a chronosequence. The researchers selected study sites along an invasion age gradient, with some sites representing older invasions by the N-fixer *Retama monosperma* (L.) and others representing recent invasions (Muñoz Vallés et al. 2011).

Studying the interaction between successional dynamics and invasive N-fixing species would also require looking beyond community-level impacts. While plant–plant interactions are a key aspect of successional change (Connell and Slatyer 1977), the regime shifts involved in catapulting a community towards

a different successional trajectory often require some fundamental alteration to ecosystem processes. Therefore, future reviews in this area would benefit from focusing on the connection between ecosystem-level impacts and community-level impacts of invasive N-fixing plants (Levine et al. 2003; Scherer-Lorenzen et al. 2007). In the case of invasive N-fixing plants, nitrogen enrichment represents one of the most prominent pathways through which such ecosystem-level change can occur (Walker and Vitousek 1989). It would be interesting to explore whether a greater magnitude of nitrogen enrichment corresponds with a greater impact on successional trajectories, and how community changes may play a mediating role in that process. Future research could therefore benefit from explicitly examining how these ecosystem-level changes translate into shifts in plant–plant interactions and successional dynamics.

One useful framework for examining these larger-scale impacts is the concept of ecosystem transformers. The term “transformer” in the context of invasive species was first coined by David Richardson, and refers to a subset of invasive plants that substantially alter the nature of an ecosystem over a large area (Richardson et al. 2000). Several of the N-fixing species covered in this review were described as transformers in the systems they invaded (Archer et al. 1988; Vitousek and Walker 1989; Hughes and Denslow 2005; Hellmann et al. 2011; Stinca et al. 2015; Vetter et al. 2018; Boscutti et al. 2020). These species were

typically described as altering both the community structure and ecosystem functioning, through a variety of mechanisms.

Although the concept of ecosystem transformers was not a central focus of this thesis, it may provide a useful lens for examining which invasive N-fixers are most likely to alter successional trajectories. There may be substantial overlap in the invasive N-fixers classified as transformers and those that have the potential to substantially alter successional trajectories. Future research could therefore either synthesize evidence or explicitly test whether invasive N-fixers classified as ecosystem transformers are more likely to alter successional trajectories than other invasive N-fixing species.

3. Invasiveness vs. impact

This review also raises a broader conceptual question concerning the relationship between the mechanisms that allow invasive N-fixing plants to establish and spread, and the mechanisms that drive their ecological impacts once established. Over the course of my literature search, it became necessary to differentiate between papers that explored the invasiveness of N-fixing plants—that is, the success of N-fixers establishing and spreading in a system—and papers examining the impact of already established N-fixers in the invaded systems. This review falls squarely in the latter category. However, there is an abundance of literature on the traits and mechanisms by which N-fixers

successfully invade systems, potentially more than exists in quantifying their impacts (Catford et al. 2019). In this case, I refer to successful invasion as both successful spread and establishment of a non-native species (Marchetti et al. 2023).

This distinction raises an interesting question: are the N-fixing species that successfully establish and spread in new environments the same species that produce the most substantial ecological impacts once established? A future review paper might approach this question by comparing the mechanisms underlying impact—as outlined in this review—to the mechanisms underlying successful invasion for N-fixing species. Such an approach could help clarify whether invasiveness and ecological impact tend to coincide specifically for N-fixing plants, or whether they represent distinct dimensions of the invasion process.

Conclusion

Invasive N-fixing species have well-documented effects on nitrogen cycling, but this review shows that their community-level impacts are best understood through the plant–plant interactions they generate. By focusing on how nitrogen enrichment shifts the balance between competition and facilitation, I identified a set of recurring pathways through which these species alter community structure and diversity.

At the same time, these interactions are highly context-dependent and change over time, contributing to the variability in impacts observed across

systems. This suggests that predicting the effects of invasive N-fixers requires not just measuring changes in nitrogen availability, but understanding how those changes translate into shifting interaction dynamics within plant communities.

Future work would benefit from more direct integration of ecosystem-level measurements with community-level responses, as well as longer-term studies that capture how these interactions evolve over the course of an invasion.

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