

Increasing Resistance and Reducing Vulnerability to Invasive Species at Sleeping Bear Dunes National Lakeshore

by

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Client Organization: Sleeping Bear Dunes National Lakeshore



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Executive Summary

Invasive plant species pose a significant threat to long-term ecosystem health, especially as new invasives continue to arise. Current invasive management strategies mainly focus on reducing or eliminating single species through chemical and physical removal methods. However, these reactive approaches are often costly, time intensive, and lack long-term success. Many practitioners are increasingly interested in a preemptive, resistance-based approach to management that focuses on actively reducing an ecosystem's vulnerability to invasion. Such an approach allows practitioners to address multiple invasives at once, increasing the efficiency, cost-effectiveness, and overall sustainability of managing invasive species. We aimed to meet the widespread need for improved understanding and ability to implement this alternative systems-based management approach, specifically as it applies to Sleeping Bear Dunes National Lakeshore (SBDNL). We used three main sources to inform our recommendations: 1) review of current research on resistance and vulnerability to invasion, 2) analysis of existing monitoring and spatial data at SBDNL related to vulnerability, and 3) perspectives and experiences of on the ground practitioners.

Literature Review

Research revealed that current species-specific management efforts involve substantial inputs of time, money, and resources without a guarantee of success; in many cases, success is hindered by secondary invasion of other non-native species. Removal efforts are also limited by negative effects of herbicide application on the native community and increases in the number and performance of invasive plant species with climate change. There are, however, factors and management techniques that would make an ecosystem more resistant to invasives over time. We found evidence that communities with natural enemies, high plant species and functional group diversity, and strong native competitors are likely to resist plant invasion, while those with resource fluctuations and extreme disturbance or high invasive propagule pressure are likely to be vulnerable. Empirical evidence demonstrated that resistance can be increased by intentional manipulation of these factors, specifically strategic seeding with natives or altering physical conditions.

Data Analysis

We used the characteristics identified in our literature review to examine site-specific drivers of vulnerability using existing spatial and monitoring data from SBDNL. Specifically, we used geographic information system (GIS) modeling in FRAGSTATS to pinpoint the areas in SBDNL that may be more vulnerable to invasion as a result of fragmentation from development. The fragmentation analysis identified two major sites in SBDNL to prioritize for management and monitoring: Benzie Corridor and the beachfront trails near Glen Arbor. Using a long-term vegetation monitoring dataset, we statistically tested the relationship between ecosystem characteristics in SBDNL and invasive species presence. We found that balsam mixed-conifer forests are significantly more likely to have more invasive species than pine forests and sugar maple/beech forests. For every one species increase in native species, the probability of an increase of one species of invasive increases by 4.23%. No significant relationship was found between the amount of herbivore browse damage and the number of invasive species.

Practitioner Perspectives

In a practitioner-tailored workshop and eight in-depth interviews with invasive managers across the Great Lakes Region, we asked practitioners: 1) What characteristics do you associate with more vulnerable or more resistant plant communities?; 2) In what ways do you take a systems-based approach and what have you learned?; and 3) What are the challenges or barriers to adopting resistance-based approaches?

Practitioners associate anthropogenic disturbances (including management and overabundant herbivores), fragmentation, and high nutrient levels with increased community vulnerability, and they associate natural disturbance regimes, connectivity, and native species diversity with increased resistance. While practitioners frequently discuss the need for systems-based strategies and do take multi-species or habitat-wide approaches, actual resistance-based techniques such as native seeding are not major components of their overall management actions. To overcome barriers to taking new approaches, practitioners identify the need for 1) site-specific research to inform resistance-based approaches, 2) increased funding for monitoring long-term effectiveness, and 3) enhancing communication with other practitioners and the public to support the paradigm shift from species- to systems-based management.

Recommendations

Based on our combined approach of reviewing current research, analyzing existing data, and hearing from practitioners, we are able to make both general and site-specific recommendations and identify directions for future research. For a more effective approach to invasive plant management at any site in the long-term, we recommend:

- Strategic seeding for functional groups, native competitors, or cover crops to build or restore ecosystem resistance to invasives.
- Minimizing resource disturbances to help prevent further invasions.
- Actively managing for a reduction in resources where anthropogenic changes in resource availability has occurred (for example due to invasive removal, widespread loss of plants from pest damage, or nutrient loading).

Specific to SBDNL, we recommend the following areas be prioritized for monitoring and resistance-based management because of their higher vulnerability:

- Mixed-conifer forest with higher invasive diversity than other forest types.
- The highly fragmented areas of Benzie Corridor and the beachfront trails near Glen Arbor.
- Forests experiencing increased resource availability due to emerald ash borer reduction of ash trees.

Priorities for future work at SBDNL and generally in the field of invasives management include:

- Increase ecosystem- and region-specific research and understanding to inform resistance-based management. This can be done through collaboration with Indigenous communities to incorporate Traditional Ecological Knowledge (TEK), experimental manipulations, public demonstration sites, and long-term monitoring. Most in need of study, based on both the literature and practitioner perspectives, are the impacts of herbivory, natural disturbances, habitat connectivity, successional stages, and nutrient extremes on vulnerability. We also recommend that SBDNL and other relevant vegetation monitoring programs include dune and coastal ecosystems and add measures of propagule pressure, resource availability, and functional group diversity.
- Interview additional practitioners and stakeholders to inform how outreach and education programs could build support and understanding of approaches that decrease whole-system vulnerability to invasion and expand measures of restoration success beyond invasive species removal.

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We would also like to acknowledge that we have the privilege of living, learning, and working on traditional Anishinaabe land. The University of Michigan originated on and continues to benefit from lands ceded to the federal government in 1817 by the Odawa, Ojibwe, Bodewadami, and Wyandot under the Treaty at the Foot of the Rapids. Our university stands on lands violently wrested from Indigenous peoples, and thus our research has inherently benefited from their exploitation. This acknowledgement is not intended to take the place of meaningful action, and we hope that these words are but an initial step toward restitution and justice.

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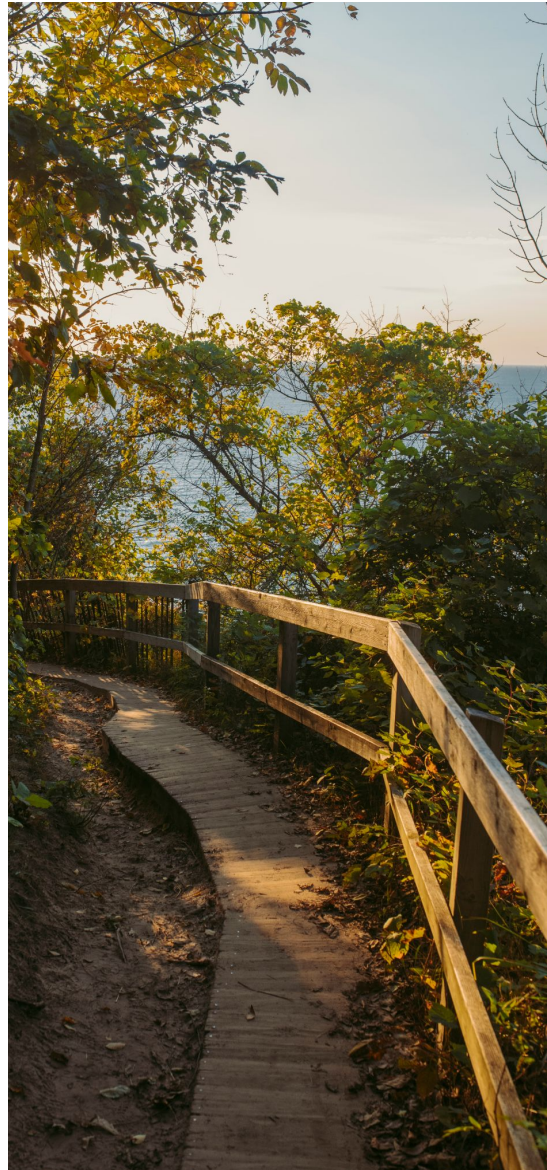


Image courtesy of Bethany Louria, 2020

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Chapter 1 | Introduction

Resistance-based invasive species management in Sleeping Bear Dunes National Lakeshore



Bethany Louria, 2020

Invasive species pose a significant threat to long-term ecosystem health, especially as new invasives are introduced through environmental and human factors (DiTomaso, 2000; Mack et al., 2000). Common invasive plant management strategies focus on eliminating single species through chemical and physical methods; however, this can be very costly and time-consuming for land managers (Kettenring & Adams, 2011; Seastedt et al., 2008). In response to this issue, we studied how to effectively manage for ecosystem-

level resistance to plant invasion and whether it can serve as a feasible alternative to single-species control efforts. Resistance-based management is a shift in focus from the invasive species to the community it invades. It involves assessing plant communities for vulnerability and implementing strategies to preempt or reduce the impact of an invasion by increasing the resistance of the community to any aggressive non-native species. This contrasts with conventional invasive species management, which mostly seeks to

eliminate or reduce invasive species during or after their establishment.

We worked with the National Park Service at Sleeping Bear Dunes National Lakeshore (SBDNL) to identify how practitioners can effectively prioritize sites for resistance-based management, as well as to determine the barriers that prevent the implementation of resistance-based management. We summarized existing research on the causes of vulnerability and resistance to plant invasion, investigated the environmental factors that predict vulnerability to invasive species using existing data and spatial analysis, and conducted interviews with practitioners across multiple organizations to better understand the perceived barriers of implementing resistance-based management.

Client and Site Background

Located in the northwestern part of Michigan's Lower Peninsula (Figure 1.1), the landscape of SBDNL is rich in cultural heritage. The United States Congress established SBDNL in 1970 with the passage of Public Law 91-479, but prior to that, this area was used by Indigenous peoples, lumbermen, sailors, and farmers. Archaeological evidence shows Indigenous

occupation of the land dating back over 3,000 years, and Ottawa and Ojibwe families migrated to the area in the 17th century to hunt, fish, and collect maple sap (Haskell & Alanen, 1994). The 1836 *Treaty with the Ottawa, etc.* federally protects the rights of five American Indian tribes to participate in hunting, fishing, and gathering activities in SBDNL. Today, the park is visited by over 1.5 million people annually for activities such as biking, hiking, dune climbing, swimming, kayaking, fishing, hunting, skiing, and snowshoeing.



Figure 1.1 | The location of Sleeping Bear Dunes National Lakeshore (Mechenich et al., 2009).

A major value of SBDNL is the diversity and uniqueness of the natural habitats it encompasses. As shown in Figure 1.2, SBDNL includes hardwood and upland

deciduous forests (57%), upland pines and conifers (3%), mixed upland forests (7%), lowland forests (6%), inland waters (2%), non-forested wetlands (3%), dunes and beaches (9%), and openlands (12%), which include historic farmland (Mechenich et al., 2009). The final 1% of the park is composed of roads, parking lots, and other developed landscapes. The most notable features are the ancient sand dunes, which are products of wind, ice, and water action over thousands of years. The lakeshore can trace its origins to the Wisconsin glaciation, which left the area 11,000 years ago (SBDNL, 2009). During this time, ice deposited sediment at glacial borders and margins. These deposits are known as end moraines and contained a mixture of rock, sand, gravel, and clay. There is an end moraine at SBDNL, the Manistee Moraine, which forms the uplands of Sleeping Bear. In fact, the dunes at SBDNL are known as perched dunes because they stand atop the glacial deposits. These perched dunes are part of the largest freshwater dune system in the world (SBDNL, 2009).

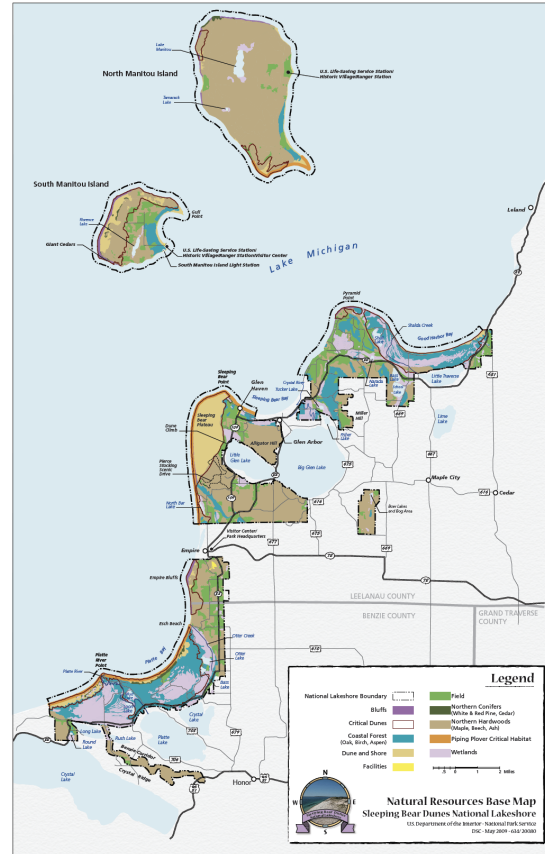


Figure 1.2 | A map of major habitats in the Sleeping Bear Dunes National Lakeshore (Sleeping Bear Dunes National Lakeshore, 2009).

The National Park Service has a general mission of preserving and protecting the natural, cultural, historical, and recreational landscape of the United States national parks. Specifically, the goal of SBDNL is to preserve the forests, dune system, beaches, and ancient glacial phenomena in the park so that these natural features can be used for public inspiration, education, and recreation (SBDNL, 2009). The National Park Service has identified three major threats to the goals of SBDNL: climate change, invasive

species, and development pressures. Invasive species are a particularly pressing issue since there are currently 240 nonnative plant species present in the park (J. Gehring, personal communication, January 22, 2020). These invasives are not restricted to limited areas but occur at over 500 different sites in the park (Figure 1.3).

SBDNL is already attempting to control and eradicate invasive species that are present at the lakeshore, following an Integrated Pest Management plan prepared by the National Park Service that identifies an array of management methods to be used by the park (Great Lakes Invasive Plant Management Team, 2020). This plan includes actions such as hand pulling and digging, mowing and cutting, spraying with selective herbicides, and the release of biocontrol insects and pathogens. However, the National Park Service aspires to utilize more alternatives to herbicide, including implementing preventive restoration. Preventive restoration is the use of practices that halt the introduction and establishment of invasive species (Great Lakes Invasive Plant Management Team, 2020). Methods include resistance-based management, which bolsters a plant community's ability to withstand invasion. Specific resistance-based management practices that SBDNL aspires to implement include the

establishment of long-term compositional and structural complexity in forests affected by the emerald ash borer (*Agrilus planipennis*) and the reintroduction of fire regimes to fire-adapted, dry northern forests and wooded swales (J. Gehring, personal communication, January 22, 2020).

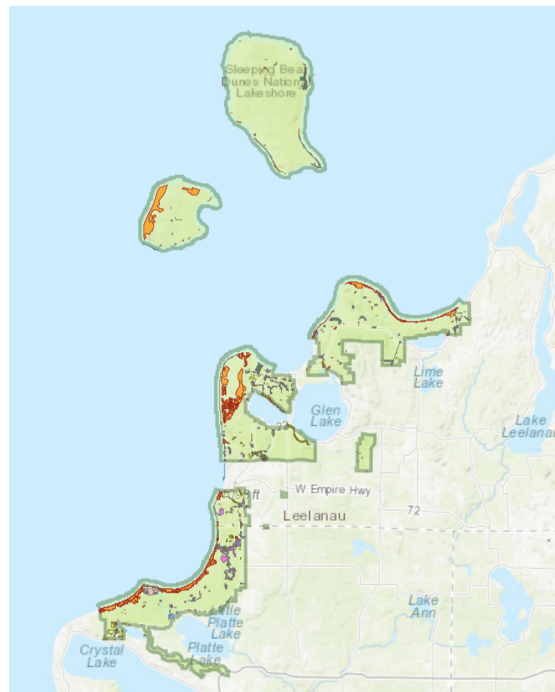


Figure 1.3 | Map of the Sleeping Bear Dunes National Lakeshore. The red and orange polygons represent the areas that contain the most abundant invasive plants (National Park Service, 2020).

Project Goals

Our project focused on enhancing SBDNL's efforts to manage invasive species through the use of resistance-based methods. To help the park transition from their current invasive species management techniques to resistance-based methods, we created and achieved four objectives, outlined below and in Figure 1.4:

1. Compile a review of current literature to determine the characteristics and practices related to plant community vulnerability and resistance.
2. Identify potentially vulnerable sites to prioritize for resistance-based management at SBDNL.
3. Understand the characteristics management practitioners associate with plant community vulnerability and resistance, and identify the barriers faced by practitioners to implementing resistance-based management.
4. Provide recommendations for how to transition to resistance-based management practices at SBDNL and any similar site managing invasive plants.

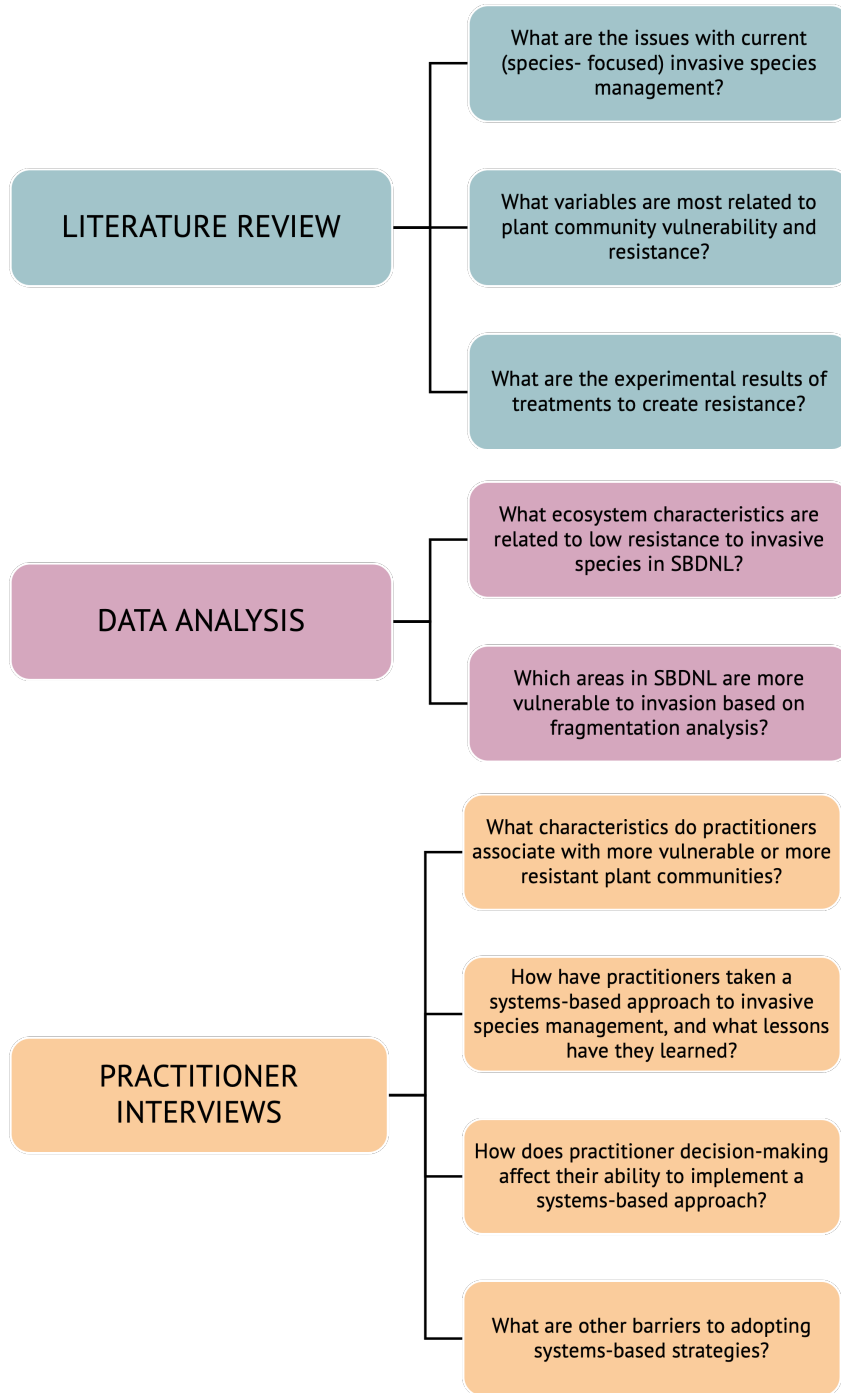


Figure 1.4 | Flowchart that depicts the branches of our project for Sleeping Bear Dunes National Lakeshore (SBDNL), as well as the core questions being investigated in each approach.

Project Significance

Our project provides SBDNL with resistance-based management recommendations for existing and future invasions in the park. A holistic, resistance-based approach will allow practitioners to address multiple invasives at once, which will increase the efficiency, cost-effectiveness, and overall sustainability of managing invasive species (Figure 1.5). Through local data analysis and information from current literature, we identify sites that are at the greatest risk for future invasions and thus should be prioritized for management. We also highlight existing barriers to the implementation of resistance-based management strategies. SBDNL can use our findings to help guide their management methods and goals in a manner that ensures the long-term health of its ecosystems.

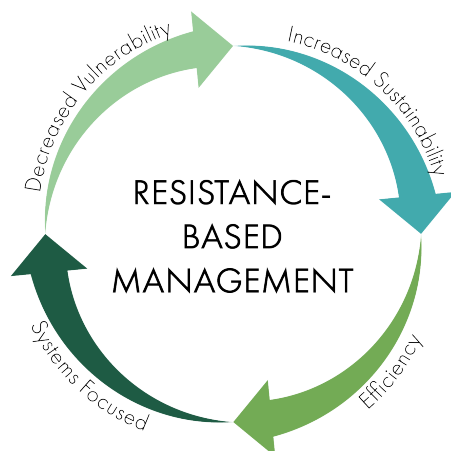


Figure 1.5 | Diagram showing the aspects of resistance-based management.

This project can reach beyond SBDNL by helping practitioners working in any ecosystem to shift their mindset from management strategies that target individual invasive species to ones that address the health of the ecosystem as a whole. Our work at SBDNL can serve as a model for invasive species management in other public and private lands, especially across the Midwest and Great Lakes region. The recommendations in this project can be modified, built upon, and applied by conservation practitioners working in other contexts.

Methods and Chapter Overview

In this report, we sequentially discuss the three approaches we took – literature review, data analyses, and practitioner interviews (Figure 1.4) – and our findings. In Chapter 2, we describe the literature review we conducted to identify the practices that research shows to be successful for managing invasive species. We looked at the limitations of current species-focused invasive plant management methods, as well as the characteristics that make plant communities more resistant to invasive plants. The specific questions we addressed were:

1. What are the known limitations of current species-focused invasive plant management?
2. What characteristics make communities more resistant or less vulnerable to invasive plants?
3. How can the results of experimental manipulations of community resistance inform future invasive plant species management?

In Chapter 3, we analytically determined which areas of SBDNL are more vulnerable to invasion so that invasion hotspots can be prioritized for management. Data analysis was divided into two sections: geographic information system (GIS) modeling and analysis of existing vegetation monitoring data. We used FRAGSTATS, a spatial pattern analysis program for quantifying landscape structure, to conduct a fragmentation analysis for the developed areas of the park and identify which areas in SBDNL might be more vulnerable to future invasion due to fragmentation. We used existing vegetation monitoring data from SBDNL to identify ecosystem characteristics that are related to low resistance to invasive species. These analyses helped to identify areas to prioritize for management in order to build natural community resistance to invasive species. Park managers can utilize these results to monitor at-risk areas more closely

for changes in invasive abundance. Both data analysis approaches contribute to the park's proactive approach to manage for resistance to plant invasion by identifying the systems-level features related to vulnerability.

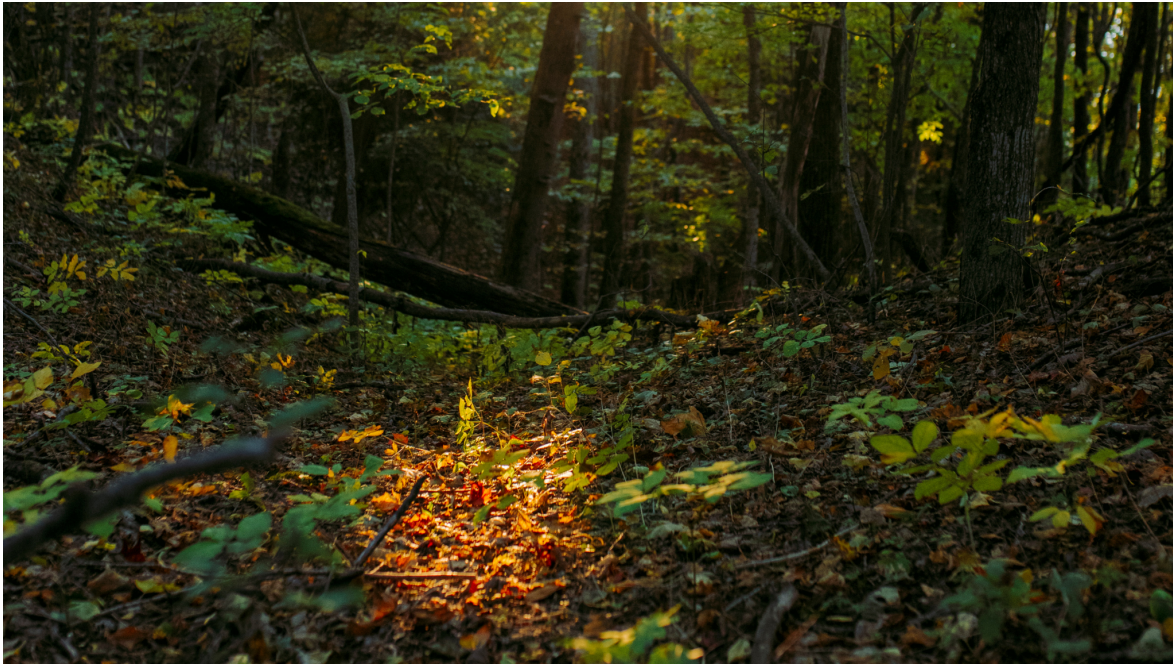
In Chapter 4 we discuss how, through a practitioner workshop and interviews, we gained practitioners perspectives on vulnerability and resistance on the ground. We discuss the extent to which practitioners are employing resistance-based management approaches and the challenges they experience. In particular, we explored how practitioner decision-making processes and structures (goal- and priority setting, funding and planning cycles, etc.) and additional limitations affect their ability to implement a systems-based approach instead of a species by species focus.

In order to have these conversations, we engaged with practitioners in two main settings: a workshop titled "Reframing Invasions: From the Invader to the Invaded" held on February 28-29, 2020 and in-depth interviews with practitioners from across various organizations in Michigan. The workshop allowed for group discussions on invasive plant management practices, characteristics of vulnerable and resistant sites, and barriers to managing invasive plants. The interviews provided a better

understanding of the needs and realities of invasive plant management from the practitioner perspective and expanded on the questions that were covered at the workshop.

Chapter 2 | Evidence from the Literature

What is vulnerability and resistance, and how can we manage for it?



Bethany Louria, 2020

The Current State of Invasive Species Management

The management and control of invasive plants is a primary focus of restoration efforts because they can have significant, adverse ecological and economic impacts. Ecologically, invasive plants can disrupt normal ecosystem functions, such as nutrient cycling and primary productivity (DiTomaso, 2000; Ehrenfeld, 2003; Heneghan et al., 2006), and affect plant diversity by displacing native species (Blossey, 1999; Ellison et al., 2005; Mack et

al., 2000). Invasive species can also have significant social and economic impacts by disrupting the recreational, cultural, and other values of natural areas and decreasing the potential economic output (Mack et al., 2000).

Common invasive plant management practices aim to reduce or eradicate a target invasive species through chemical, manual or biological treatments (Mack et al., 2000). Conventional methods include herbicide application, mowing, cutting, burning, hand pulling, mulching, grazing, and tilling

(Kettenring & Adams, 2011). Manual techniques, especially slashing and hand-felling, are often more labor-intensive (Byun et al., 2018). Biological control is the introduction of a specialized natural enemy of an invasive species to the ecosystem of interest in order to specifically control a target invasive species (Mack et al., 2000).

Overall, current species-specific invasive management efforts involve substantial inputs of time, money and resources, without a guarantee of successful eradication or even reduction of impact (Figure 2.1). For example, from 2005 to 2009, U.S. conservation organizations spent more than \$4.9 million per year on the management of just one invasive species, *Phragmites australis* (Martin & Blossey, 2013). In a review of control efforts for over 100 invasive plant species, Kettenring and Adams (2011) found that even when invasive plant cover was reduced, there were only limited gains in native species recovery. Many practitioners are recognizing the need for alternative approaches to managing current and future

invasive species (Schuurman et al., 2020; Simmons, 2005).

To address the need for alternate approaches to invasive species management, we reviewed available research to answer the following questions:

1. What are the known limitations of current species-focused invasive plant management?
2. What characteristics make communities more resistant or less vulnerable to invasive plants?
3. How can the results of experimental manipulations of community resistance inform future invasive plant species management?

Through this review, we aim to provide up-to-date and accessible information that will assist managers in shifting paradigms from focusing on removing individual invasive species, to managing for natural communities that can better resist the impact of current and even unknown future invasive plants.

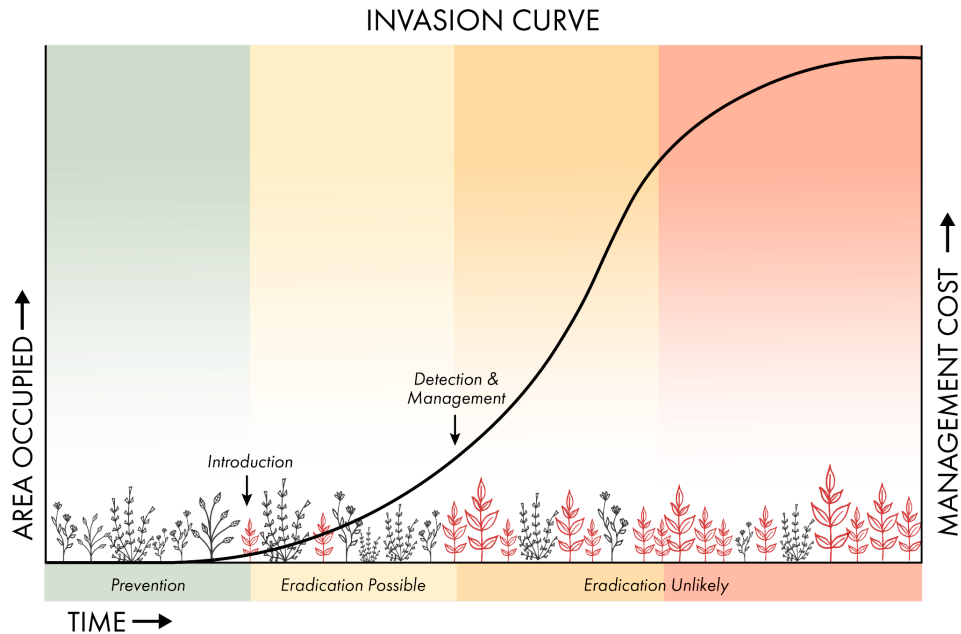


Figure 2.1 | Graphic showing the “invasion curve” indicating that over time, feasibility of eradicating invasives decreases until it is unlikely to successfully eradicate the invasive. As the area occupied by the invasive species grows, so does the cost of management. The arrows indicate the points at which invasive species are introduced to the system and when practitioners usually begin management to treat the invasive.

What are the known limitations of current species-focused invasive plant management?

I. Invasive plant removal efforts may promote secondary invasion due to resource availability and persistent seed banks.

In part, targeted invasive plant management efforts may fail due to secondary invasion, or “management-mediated invasion,” which is the increase in abundance of a non-native species after management to control another invasive species (O’Loughlin & Green, 2017; Pearson

et al., 2016). In the literature, 44% of invasive species control efforts in National Park sites (Abella, 2014), 50% of Australian management cases (Reid et al., 2009), and 75% of cases in a broad review (Pearson et al., 2016) documented challenges with secondary invasion. It may be the product of legacy effects of a previous invader (such as soil chemistry changes, which are difficult to manage directly), but especially by the increased disturbance and/or resources associated with methods used to remove the invader (O’Loughlin & Green, 2017).

Single species-focused management strategies can unintentionally cause

secondary invasions through removal practices that free up specific resources or niches. These practices include selective processes such as hand-pulling, cutting, biological control, and specific application of herbicide. For example, a study in Montana used herbicide to control spotted knapweed (*Centaurea stoebe*; Figure 2.2). Herbicide caused the reduction of target species but also resulted in reduced native forb cover and ultimately led to a secondary invasion of cheatgrass (*Bromus tectorum*) (Ortega & Pearson, 2010). Similarly, herbicide control of the invasive Amur honeysuckle (*Lonicera maackii*) with the cut/paint method in an Ohio forest caused light levels to increase 24 times more than the control. In the following years, secondary invasion of both garlic mustard (*Alliaria petiolata*) and Amur honeysuckle seedlings occurred in the treated plots (Cipollini et al., 2009). Non-selective management that promotes the opening of forest canopies to facilitate native species regeneration, such as the use of different harvesting techniques and prescribed burns, can also lead to secondary invasions (Huebner et al., 2018). Kettenring and Adams (2011) reviewed 355 studies that primarily utilized herbicide, cutting, and burning as invasive control measures. Over 25% of the evaluated

studies resulted in an open niche leading to secondary invasion of exotics.

Persistent invasive seed banks make it likely that any disturbance results in re-invasion of the target or other non-native species. Soil seed banks act as reservoirs of propagules for invasive species and can aid in their establishment and persistence (Gioria et al., 2019). The formation and function of seed banks plays a vital role in the dispersal of invasive species through time due to dormancy. One study, based on 1,149 observations for 162 species in eight habitat types, found that invasive species exhibited a higher probability of forming a persistent seed bank than non-invasive plants (Gioria et al., 2019). The removal of target species, therefore, may result in the immediate secondary invasion of those species present in the seed bank. In a densely invaded ecosystem, the seed bank can outline which species will play a key role in the recovery of the system after control of invasive species.

II. Herbicide use can have non-target impacts on native diversity, growth, and community composition.

Diversity Reduction

Evidence has shown that the use of herbicides in invasive species management harms native species by reducing the diversity of the native community. In a study by Flory and Clay (2009), post- and pre-emergent, grass-specific herbicides (fluazifop and pendimethalin, respectively) were used to remove Japanese stiltgrass (*Microstegium vimineum*). Although these herbicides were effective in killing Japanese stiltgrass, they also reduced the graminoid richness of the native community.



Figure 2.2 | Spotted knapweed (*Centaurea stoebe*) growing on a dune in SBDNL (Bethany Louria, 2020).

Growth Reduction

Another non-target effect of herbicides is growth reduction of the native plant community. Boutin et al. (2014) showed that there were delays in flowering and reduced seed production for woodlot plants in Ontario that were sprayed with fluroxypyr, mecoprop-P, metsulfuron methyl and glyphosate, glyphosate, or foramsulfuron + iodosulfuron at the seedling or reproductive life stage. The plants that were the most sensitive were those sprayed at the reproductive stages. Similarly, Crone et al. (2009) found that one application of picloram reduced flowering and the amount of seeds produced in arrowleaf balsamroot (*Balsamorhiza sagittata*) for four years. These unintended effects on native species are concerning given the prevalence of herbicide use in invasive treatment.

Growth reduction has also been observed in the offspring of plants that were exposed to herbicides. Qi et al. (2018) conducted an outdoor pot experiment that looked at the offspring of native velvetleaf (*Abutilon theophrasti*) following sublethal exposure of the parent to atrazine. Native velvetleaf seedling growth was stunted when the parent plants were exposed to the herbicide. Young et al. (2002) observed seed failure in native tall wheat grass for three consecutive years after one application of

chlorsulfuron, indicating that chlorsulfuron residues persist in the soil. Studies have also been conducted to mimic the non-target effects of herbicide application which occurs when particles fall outside of the target area. To represent herbicide drift, Wagner and Nelson (2014) applied low concentrations of picloram to dry grassland seedlings. Low concentrations of picloram suppressed seedling emergence in 14 dry grassland species. Furthermore, picloram had a negative effect on both monocot and dicot seedlings, although it is marketed as a dicot-specific herbicide. These studies demonstrate that herbicide application has the ability to reduce growth of native species over several generations, resulting in long-term consequences for an ecosystem.

Community Shift

The application of herbicides is observed to cause shifts in community composition, which can cause cascading changes in fungal and bacterial communities. Aquatic organisms can also be affected by terrestrial herbicide application. Through spray drift, runoff, and soil erosion, herbicide can enter the aquatic environment. Widenfalk et al.'s (2008) study on the effects of herbicides on the bacterial community in freshwater sediments

revealed that glyphosate shifts bacterial community composition in small but nonetheless consequential ways.

Weidenhamer and Callaway (2010) note that the functional diversity of soil bacterial communities can be reduced by 2, 4-D and glyphosate. These herbicides can also alter the functional structure of the soil bacterial community and increase the microbial biomass carbon.

III. Climate change may increase both the number and performance of invasive species, making continuous species-focused management unsustainable.

Increase in Number of Invading Plants

Climate change is likely to increase the number of new invasive plant species invading communities (Bradley et al., 2019), thus making “species by species” approaches to management or control even more challenging in the long-term. Climate change may increase the number of invasive species in an area through range expansion and the awakening of sleeper species. As northern latitudes continue to see an increase in temperature and precipitation under climate change, invasive species will shift their ranges northward and upward in elevation (Bradley et al., 2019;

Frank & Just, 2020; Kleinbauer et al., 2010), thereby exposing northern ecosystems to new invasive species. For example, northern expansion is predicted to occur for Japanese knotweed (*Fallopia japonica*; Beerling et al., 1995). Although accessible web-based models exist for predicting such range expansions (University of Georgia, n.d.), these tools further support the need for shifting away from a single-species approach, highlighting the overwhelming number of predicted incoming species in the coming years.

Climate change will also increase the number of potential invaders by providing an opportunity for naturalized species, also known as sleeper species, to become invasive if climate becomes favorable for their population growth (Bradley et al., 2018). Sleeper species can also result from native species exhibiting aggressive characteristics and becoming dominant due to environmental change such as disturbance or climate change (Frank & Just, 2020). For a native sleeper species, aggressive characteristics typically associated with invasive species, such as range expansion and phenotypic change, may occur. Although documentation of sleeper species is limited in the United States, sleeper species have been recorded in Britain. After being naturalized for over

50 years, Oxford ragwort (*Senecio squalidus*) spread across the island, taking on invasive qualities (Groves, 2008).

Improved Performance of Invasive Plants

Climate change can also increase invasive plant performance through longer growing seasons, which can in turn increase their competitiveness and make it even more important to identify management techniques that ensure a more resilient ecosystem. Warmer temperatures associated with climate change will increase the length of the growing season, thus potentially promoting invasive plants by allowing them to green-up earlier and brown-down later than usual (Bradley et al., 2019). At the University of Michigan's Biological Station in Emmet County, Michigan, Welshofer et al. (2018) tested two heavily invaded plots for the effects of warming on three invasive species: poverty oatgrass (*Danthonia spicata*), spotted knapweed (*Centaurea stoebe*), and Kentucky bluegrass (*Poa pratensis*). By warming plots to 1.8°C above ambient temperatures, the abundance of the three invasive plants increased by 19%, while abundance of native species decreased by 31% in one plot. The invasive species experienced earlier spring green-up by approximately

one day and earlier flowering by approximately two days.

Resistant ecosystems are ***less likely to allow for the dominance or significant impacts of invaders*** and are ecosystems that can ***maintain function and structure*** even with the introduction of non-native species.

From the invader to the invaded: What characteristics make communities more resistant or less vulnerable to invasive plants?

The likelihood of re-invasion after removal, the non-target effects of herbicides, and the unending threat of new invasive species in the face of climate change make a continuous single-species approach to invasive plant species management both ineffective and unsustainable. An alternative paradigm is to focus instead on the characteristics of the invaded community that contribute to an ecosystem's vulnerability or resistance to the establishment and proliferation of invasive species. A vulnerable ecosystem is one that may be frequently invaded by non-

native species and sees native displacement by invaders. Resistant ecosystems are less likely to allow for the dominance or significant impacts of invaders and are ecosystems that can maintain function and structure even with the introduction of non-native species.

The main components of ecosystem resistance, termed biotic and abiotic resistance, are part of a series of factors that can prevent invasion or impact, yet they usually are not the focus of control efforts (Figure 2.3, Byun et al., 2018). The first phase of invasion is introduction, which depends both on the ability of the plant to physically reach a particular location (often as the result of nursery practices or unintentional transport) and the number of plants or seeds that are introduced ("propagule pressure"; Byun et al., 2018; Colautti et al., 2006; Lockwood et al., 2005). The initial colonization and early establishment phases of an invasion are often the primary management targets because these periods represent the most vulnerable life stages for many invasive plants (Byun et al., 2018; Fraser & Karnezis, 2005). For example, Early Detection Rapid Response (EDRR) control efforts focus on these stages by fastidiously removing early arrivers before they establish (Reaser et al, 2020). Once an invasive population is

established, the ongoing costs for invasive species management can significantly increase, and the population can reach a level where it is nearly impossible and financially unfeasible to completely remove (Byun & Lee, 2017) or to restore native plant community composition and diversity (Reid et al., 2009). Biotic and abiotic resistance are the critical features of a community itself that have the potential to significantly and effectively prevent establishment, expansion, or reinvasion after removal (Byun et al., 2015).

resistance of a community in ways that can inform management of these factors. Defined broadly, biotic resistance refers to the ability of competitors, herbivores, and pathogens in a resident community to resist or limit invasion by non-native invaders (Catford et al., 2009; Levine et al., 2004; Lodge, 1993). Abiotic constraints occur when physical conditions limit the ability of an invasive species to thrive; these factors include temperature, light, water, and nutrient availability (Byun et al., 2015; Chytrý et al., 2008). Below, we elaborate on the six characteristics most cited in the literature as increasing resistance (biotic resistance due to natural enemies, plant species and functional group diversity, and strong native competitors) or vulnerability (resource availability, human disturbance and fragmentation, propagule pressure, and priority effects of seeds; Table 2.1).

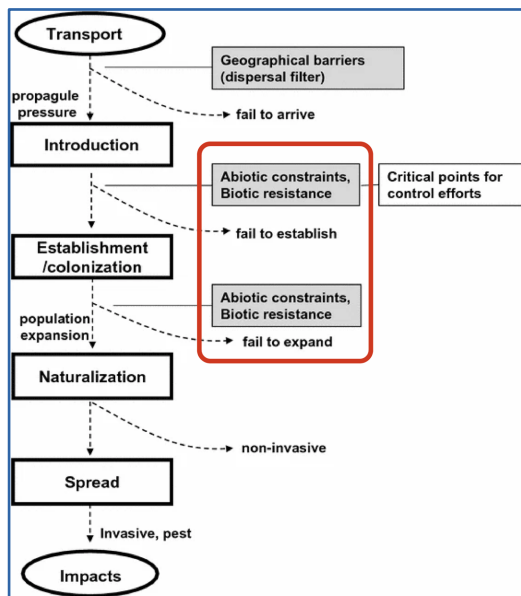


Figure 2.3 | Invasion phases showing invasion stages on the left in white and barriers to invasion on the right in grey, with opportunities for resistance-based management interventions circled in red (adapted from Byun et al., 2018).

In this section, we describe what is known about how biotic and abiotic resistance affect the overall vulnerability or

Table 2.1 | Characteristics of resistant vs. vulnerable ecosystems.

Resistant	Vulnerable
Presence of natural enemies	Resource availability
High species and functional diversity	Human disturbance and fragmentation
Strong native competitors	High invasive propagule pressure

I. Biotic resistance through natural enemies

An essential component of biotic resistance is the ability of the community to reduce the success of an invader through natural enemies that act as a control on the species' growth, such as herbivores and pathogens. In the case of invasive species, it is possible that natural enemies are transferred with the invader or that enemies are present in the receiving ecosystem. Natural enemies that enact a control on an invader contribute to the biotic resistance of an ecosystem; however, invaders often experience a reduction in enemies in comparison to their native counterparts. The Enemy Release Hypothesis (Keane & Crawley, 2002) states that plant species, on introduction to an exotic region, should experience a decrease in regulation by herbivores and other natural enemies, resulting in an increase in distribution and abundance. Byun et al. (2018) identify three main lines of evidence that support the influence of competitive release on invasive success: (1) studies show less damage from enemies on invasive species farther from their native range, (2) studies show less damage on invasive species compared to their native counterparts in the same

ecosystem, and (3) the success of some biological control programs. These patterns are further supported by a recent global meta-analysis that found invasive species strongly benefit from the absence of herbivory, while native plants have a neutral response (Ibáñez et al., 2021). On the other hand, herbivores have been shown to decrease invader establishment and performance, though plant communities are unlikely to resist exotic invasions through herbivory alone (Levine et al., 2004).

The reduction in natural enemies that benefits invasive species also applies at the microscopic level. Mitchell and Power (2003) compiled geographic data on plant associations with viruses and fungi and found that 84% fewer fungi and 24% fewer virus species infect each plant species in its naturalized versus native range. In addition, invasive plant species that are more completely released from pathogens are more widely reported as harmful invaders of both agricultural and natural ecosystems (Mitchell & Power, 2003). The absence of natural enemies, including fungi and viruses, contributes negatively to the biotic resistance of an ecosystem, and therefore ecosystem resistance overall. Introduced biocontrol measures can be one aspect of increasing biotic resistance; however, this is

generally a species-specific approach and would not broadly increase biotic resistance across all levels of an ecosystem.

To increase or maintain biotic resistance of a community, **it is essential to maintain the natural assemblage of functional groups** or the highest functional group richness.

II. Biotic resistance through plant species diversity and functional group diversity

In theory, “limiting similarity” posits that the more species present in a community, the less likely it is for an invader to have an available niche (MacArthur & Levins, 1967). Several studies have confirmed that higher species diversity contributes to biotic resistance and reduces the growth of invaders (Byun & Lee 2017; Fargione & Tilman, 2005; Frankow-Lindberg et al., 2009). However, functional group richness is considered a better predictor of invasion resistance than species diversity alone (Byun et al., 2013; Byun et al., 2018; Funk et al., 2008; Pokorny et al., 2005; Symstad, 2000). Functional groups are groups of species whose traits, in morphology and/or phenology, are similar to each other (Byun

& Lee 2017; Hooper & Dukes, 2004). Plant communities with high functional group richness are thought to be more resistant to invasion due to complete niche occupation of resources, which restricts the exploitation ability of an invasive plant (Byun & Lee, 2017; Fargione et al., 2003; Leffler et al., 2014; Pokorny et al., 2005). Pokorny et al. (2005) found that even after minimizing disturbance in plots where vegetation was removed, native assemblages where no species were removed were the most resistant to invasion, with the functional group of forbs having the largest influence. In a restoration context, focusing on the *functional* diversity of the restored community seems a promising approach when facing multiple invaders and/or fluctuating abiotic conditions and could inform species selection for restoration (Byun et al., 2018).

Some functional groups are more resistant to invasion than others, but which one depends on the functional group of the invasive. Byun and Lee (2017) found that the functional group containing fast-growing annuals resulted in the highest biotic resistance to invasion by white snakeroot (*Ageratina altissima*). Similarly, Pokorny et al. (2005) investigated invasion resistance of plant functional groups against spotted knapweed and found that forb removal

increased plant community vulnerability the most due to the similar ecological demands of invasive and native forbs. To increase or maintain biotic resistance of a community, it is essential to maintain the natural assemblage of functional groups or the highest functional group richness (Pokorny et al., 2005).

The theory that a species-rich community is more resistant to invasive species can extend to the seed bank level. Certain seed bank attributes such as species richness, species composition, and seed density can help in determining the resilience of an invaded ecosystem. Frieswyk and Zedler (2006) characterize a resilient seed bank as containing high densities of native species, whereas a degraded seed bank contains a higher proportion of invasive seed densities. In a densely invaded ecosystem, the seed bank can outline which species will play a key role in the recovery of the system after control of invasive species or any disturbance that makes resources available. Therefore, intentional seeding may be an effective treatment to increase species richness, and therefore resistance, in an ecosystem.

III. Biotic resistance through strong native competitors

The reason for the influence of species and functional group diversity on biotic resistance is competition for resources, so simply the presence of strong native competitors can also increase resistance to invasion. Successful invader establishment depends on either a fitness advantage or niche difference from resident species (MacDougall et al., 2009). Niche differences increase the probability of invasive establishment, but superior fitness allows invaders to become dominant in an ecosystem (MacDougall et al., 2009). High levels of competition from native species have the potential to prevent invasive species from establishing in an area due to different competitive dynamics including phenology, light, space, and below-ground competition (Gioria & Osborne, 2014). A robust meta-analysis by Levine et al. (2004) revealed that strong resident competitors significantly reduced the establishment *and* performance of exotic invaders.

IV. Vulnerability due to resource availability

Any situation that ***alters or increases the availability of resources*** in an ecosystem could ***increase vulnerability to invasion***.

In addition to biotic resistance, abiotic constraints of an ecosystem are a large component of ecosystem resistance to invaders. Abiotic constraints are a form of ecosystem resistance where the *physical* conditions of the ecosystem limit the success of an invader (Collinge et al., 2011). Any situation that alters or increases the availability of resources in an ecosystem could increase vulnerability to invasion. Resources of an ecosystem include abiotic characteristics such as light and nutrient availability, space, and amount of soil water. Fluctuations in resource availability may modify the abiotic environment to favor conditions for non-native species, providing invasion opportunity (Hobbs & Huenneke, 1992). Assuming that resources are fully utilized under “normal” conditions, a disturbance that increases resource levels, such as eutrophication, provides an opportunity for invasion. A decrease in resource use, like a die-off of resident

plants, may have the same effect (Catford et al., 2009).

One especially clear trend across the literature is that high levels of nutrient input support the invasion of non-native species. Invasive species have been shown to benefit more than native species following an increase in nutrients, and few non-native species are found in environmentally extreme and nutrient-poor habitats (Chytrý et al., 2008; Ibáñez et al., 2021). In contrast, man-made habitats, or those frequently disturbed with fluctuating nutrient availability, have higher proportions of non-native species (Chytrý et al., 2008).

Phragmites australis, an aggressive coastal invader in North America, has been shown to increase in density, height, and biomass of shoots after biotic disturbance of neighboring vegetation and addition of nutrients to a marsh (Minchinton & Bertness, 2003). Alarming, biomass of the matrix vegetation decreased with increasing severity of disturbance (Minchinton & Bertness, 2003). These alterations follow a plausible anthropogenic disturbance model, where coastal land is cleared, and nitrogen runoff from farms and fertilizer may increase. Globally, there are similar patterns of nitrogen enrichment stimulating invasive plant species among habitats in different regions and continents (Byun et al., 2018).

Trends for other resource disturbances are not as clear, but studies have connected changes in light and water availability to abiotic ecosystem resistance. Invasive plants tend to benefit more in terms of growth from an increase in light than native species (Ibáñez et al., 2021). Three tree species invasive to the northeastern US (*Ailanthus altissima*, *Alliaria petiolata*, and *Microstegium vimineum*) are more likely to germinate under conditions of greater canopy opening (Huebner et al., 2018). Invasive species have the ability to exploit available resources that disturbances provide.

The effect of fluctuating water resources on invasibility depends on the ecosystem. For example, flooding directly reduced invasion success of *Phragmites australis* in plots with wetland species (Byun et al., 2015), while flooding of a forest understory significantly facilitated invasion by non-native species (Von Holle & Simberloff, 2005). Facilitation of invasive species was found to occur in vernal pools in a California grassland (Collinge et al., 2011). Low-water conditions increase the competitive ability of native species in some cases and invasive species in others (Gioria & Osborne, 2014). Over multiple studies, decreasing water resources tend to benefit invasive species

significantly more than native plants (Ibáñez et al., 2021).

V. Vulnerability due to human disturbance and fragmentation

Invasive species tend to outperform native species after **disturbance caused by human activities**, including management activities.

Invasive species tend to outperform native species after disturbance caused by human activities (e.g., pollution, edge effect, trampling, hiking), including management activities (Ibáñez et al., 2021). The success of invasive species after a disturbance may be due to changes in resource availability (as discussed in the previous section) or may be due to landscape-level habitat alteration. As human development alters the size and configuration of natural habitat, it drives invasion. Fragmentation, one of several components of human-mediated disturbance, is the process whereby ecosystem loss results in the isolation of small remnant ecosystem patches that were formally continuous and large (Saunders et al., 1991; Vila & Ibáñez, 2011). Fragmentation generally increases the

amount of edge area and decreases the amount of core, or interior, habitat available to biota (Saunders et al., 1991).

Fragmentation can also increase the distance that native species have to disperse to reach suitable habitat via wind (Soons et al., 2005). It is hypothesized that landscape configuration (e.g., the presence of transport corridors or edges) is of primary importance to the arrival and establishment of alien species; this is heavily influenced by fragmentation. In their 2011 literature review, Vila and Ibáñez found a sharp decline in the level of invasion by exotic plant species of a patch from the fragment edges to the interior of the patch, suggesting lower levels of ecosystem resistance near the edge of a patch than in the interior. For example, as improved, paved roads replace natural habitats, they increase invasibility of adjacent ecosystems in the western US (Gelbard & Belnap, 2003). In a study of a managed northern hardwood forest, exotic species were most prevalent within 15m of unpaved roads, whereas they occurred infrequently in the interior forest (Watkins et al., 2003). Other studies (Hansen & Clevenger, 2005; Mortensen et al., 2009) similarly report decreased abundance of invasive species away from transportation corridors in forests.

VI. Vulnerability due to propagule pressure and priority effects of seeds

If an ecosystem is saturated with seeds of an arriving invasive, the probability of establishment may overcome ecosystem resistance. The extent of invasives' arrival is measured as propagule pressure, a concept that incorporates both the quantity and frequency of arrival of propagules (Lockwood et al., 2005). Propagules include seeds, as well as ramets or vegetative reproductive structures, and can arrive from elsewhere or be present in the soil or seed bank. Increasing propagule pressure has been strongly associated with their spread and success (Byun et al., 2018; Colautti et al., 2006; Ibáñez et al., 2009; Lockwood et al., 2005). In a four-year field experiment with forest understory plants, alterations to the physical environment and the number of established resident species had negligible impact on habitat invasibility in comparison to propagule pressure (Von Holle & Simberloff, 2005). Colautti et al. (2006) confirm the importance of propagule pressure in invasion success in a meta-analysis of invasive characteristics and habitat invasibility. They found propagule pressure to be a significant predictor of both invasiveness and invasibility in 55 of 64 total cases.

Propagule pressure can also directly influence the priority effect, which is the increase in the proliferation of a species that arrives first to an available area (Collinge & Ray 2009, Drake et al. 1993). High propagule pressure can allow species to establish earlier than others, but differential competitive abilities can also mitigate the strength of priority effects, allowing some late-arriving species to still succeed in a community (Stuble & Souza, 2016). Invasive species may have stronger priority effects than natives, even when propagule pressure is equal. Dickson et al. (2012) found that invasive species formed near-monocultures when seeded first, resulting in 97.5% of total biomass. Native species did not similarly dominate, even when seeded first, totalling only 29.8% of total biomass. On the other hand, Byun et al. (2013) found that some native annual plants grew faster than the invasive *Phragmites australis*, suggesting priority effect of native species is possible by pre-empting niche occupation and inhibiting slower growing species (Byun et al., 2013). Biotic resistance from the prior establishment of resident plant cover could lower the threshold at which propagule pressure of an introduced species leads to invasion (Byun et al., 2015). Early intervention prior to establishment of

invaders is important to achieve the most benefits from biotic resistance. Below, we discuss how increasing native species through intentional seeding or planting could be used to bolster community resistance to invasion.

How can the results of experimental manipulations of community resistance inform future invasive plant species management?

We have reviewed the evidence that communities with natural enemies, high plant species and functional group diversity, and strong native competitors are likely to resist plant invasion, while those with resource fluctuations and disturbance or high invasive propagule pressure are likely to be vulnerable. If we desire to shift the focus from managing invasive plants to managing these community traits, what do these findings mean in practice? How can restoration practices and efforts to prioritize areas for protection operationalize community characteristics of resistance and vulnerability for long-term invasive species management? While methods to increase resistance may be ecosystem-specific, we provide some experimentally tested examples and related recommendations of

the following general approaches: native seeding and resource disturbance minimization.

I. Seeding and plant cover to increase biotic resistance and overcome invasive propagule pressure.

Especially in areas with high invasive propagule pressure, ***strategic native seeding may be key to increasing ecosystem resistance.***

Seeding native species is a viable method to increase long-term biotic resistance of an ecosystem by increasing resource competition with current or future invaders. Especially in areas with high invasive propagule pressure, strategic native seeding may be key to increasing ecosystem resistance. The selection of plants for seeding and cover is important, as randomly adding native species to increase diversity may not increase ecosystem resistance and may even increase vulnerability to invasion (Byun et al., 2018). To inform seeding strategy, it is recommended to collect data on the environmental constraints of the site and traits associated with resource use and

competitive ability of native and invasive species (D'Antonio et al., 2016). Collected data may inform which strategic seeding approach may be the most successful in any given ecosystem: seeding for absent functional groups, seeding with hypothesized native competitors, or seeding cover crops. Additionally, if priority effects are found to have a strong influence on the competitive ability of invasive plants in a particular area, it may be necessary to concentrate seeding at the beginning of the growing season and shortly after disturbance (Dickson et al., 2012).

The identification of which functional groups are present and absent informs the type of seeding that would most increase biotic resistance via complementarity. Researchers have classified groups of plants into functional groups based on functional traits and cluster analyses. For example, Byun et al. (2013) classified wetland species into functional groups based on traits utilizable in relating functional group identity with biotic resistance using the TRY global database of plant traits. The traits identified include longevity, seed dry mass, specific leaf area, leaf nitrogen content, relative growth rate, growth form, leaf dry matter content, and height at maturity (Byun et al., 2013). Seed mixtures with combined functional groups experienced

higher biotic resistance than monocultures against the invasive *Phragmites australis*; fast-growing annuals were the most resistant functional group (Byun et al., 2013). Their methodology provides a good baseline for those hoping to evaluate functional groups present in an ecosystem. Funk et al. (2008) recommend examining functional traits of seedlings as well as adults to reveal more about patterns of competition and coexistence of species because seedlings are more vulnerable to stresses compared to adult individuals. Consistent evidence for the importance of functional group diversity in biotic resistance (Byun et al., 2013; Byun et al., 2018; Funk et al., 2008; Pokorny et al., 2005; Symstad, 2000) confirms that seeding for absent functional groups should be prioritized for effective invasive species management. Following this recommendation requires that managers first have a good knowledge of which species are present and their functional characteristics, so functional gaps could be identified by combining a chart of species characteristics with monitoring data on abundance over time.

In the absence of community-level functional group data, biotic resistance can also be achieved by seeding native species hypothesized or known to be in direct

resource competition with an invader (Funk et al., 2008). Simmons (2005), for example, seeded the native Indian blanket (*Gaillardia pulchella*) with invasive turnipweed (*Rapistrum rugosum*) based on a hypothesized similar niche. Seeding reduced growth of the target species, suggesting that sowing competitive native seeds at high densities can reduce the success of incoming invasive species (Simmons, 2005). Rather than seeding with one particular alternative species, developing a seed mixture that contains three or four competitive native species will lead to a diverse plant community that can maintain biotic resistance in a changing environment and prevent re-invasion (Byun & Lee, 2017).

Finally, simply increasing the density of plant cover via seeding or planting can reduce invasibility of an ecosystem. Cover cropping with five native species (annuals or short-lived perennials) reduced the maximum cover of the invasive reed canary grass (*Phalaris arundinacea*) from greater than 75% to less than 24% (Iannone & Galatowitsch, 2008). Similar results were found in a greenhouse study of western grasslands, and researchers reported more beneficial outcomes from annual cover crops than perennials (Perry et al., 2009). One caveat to this success is that the cover

crops also reduced establishment of some native species (Iannone & Galatowitsch, 2008). Cover cropping is an attractive management strategy as plant cover can be self-maintaining, so repeated control interventions become less necessary, yet monitoring is recommended (Byun et al., 2018).

II. Minimizing physical and resource disturbances to decrease ecosystem vulnerability during management.

Managers should **avoid practices that increase light and nutrients** or even **actively manage for a reduction in resources**.

Given that disturbance and available resources are known to increase vulnerability to invasion, physically disruptive removal of vegetation should be avoided, especially when invasive propagule pressure is high. When vegetation must be removed from an ecosystem, management should ensure the availability of propagules from competitive native species and use the least disruptive seeding methods. No-till range drills, for example, have been utilized in revegetation studies that seek to

minimize soil disturbance (Sheley et al. 2006).

To avoid a competitive advantage that invasive species may gain from resource fluctuations, managers should avoid practices that increase light and nutrients or even actively manage for a reduction in resources. This is particularly important in ecosystems with a history of anthropogenic nutrient loading through farming or runoff. Some studies have found that adding carbon in the form of sucrose or sawdust lowers the amount of available nitrogen in the soil, thereby favoring native species (Byun et al., 2018). Sucrose applications temporarily reduced soil nitrate to inferred pre-colonization levels in woodlands, dramatically reducing growth of exotic annuals and enhancing native perennial abundance in Australia (Prober et al., 2005). Applying sawdust to decrease the available nitrogen in the soil reduced the seedling establishment of invasive reed canary grass (*Phalaris arundinacea*) by 61% (Iannone & Galatowitsch, 2008). The effects of the sawdust were negligible after 18 weeks, suggesting that this treatment could reduce establishment without a long-term effect on soil composition. Overall, implementing minimally-disruptive or resource-reducing management practices can prevent or reduce the severity of future invasions.

Conclusion

Species-focused management approaches may not address the ***underlying issues of the plant community*** that make the community ***susceptible to repeated invasions***.

Resistance-based methods are not the norm in invasive species management (Kettenring & Adams, 2011), but there are several lines of evidence that support the need to shift from a reactive focus on reducing certain species to a proactive building of whole community resistance to invasion. The attempted control of invasives through species-focused removal can have non-target effects and even result in environmental conditions that promote reinvasion or new invasions (Hobbs & Huenneke, 1992), especially in the presence of high propagule pressure. Additionally, the continued rise of new invasive species associated with climate change make a species-by-species approach unsustainable.

We identified several characteristics of the invaded community that contribute to an ecosystem's vulnerability or resistance. Factors found to contribute to resistance include biotic resistance due to natural

enemies, plant species diversity and functional group diversity, and strong native competitors. Characteristics shown to contribute to vulnerability include resource availability, human disturbance and fragmentation, and propagule pressure and priority effects of seeds.

Knowing the factors influencing vulnerability and resistance of a particular site can allow for active and tailored management to reduce or prevent invasive impact in the long-term. We identified several actions that have been shown to effectively build or restore ecosystem resistance to invasion, including strategic native seeding, minimizing disturbance, and actively reducing resource availability. We provide additional examples of management strategies that apply specific mechanisms of vulnerability and resistance in a two-page practitioner summary in Appendix A.

Species-focused management approaches may not address the underlying issues of the plant community that make the community susceptible to repeated invasions. Recognizing the relative influence of community-level characteristics on invasion outcomes can significantly aid decision-making and management resource allocation, as well as inform practitioners of the limitations of certain management

techniques. Also, since a single factor rarely governs invasion success, multiple drivers must be addressed simultaneously (Byun et al., 2018), making more than one approach suitable, or even necessary, for a given site. The recommended resistance-based management methods, even when combined with more conventional practices such as herbicide and mowing, have the potential to increase an ecosystem's long-term resistance to invasion.

Chapter 3 | Applications to SBDNL

Which areas have high vulnerability to invasion based on existing data?



Bethany Louria, 2020

While the literature may identify several factors known to increase resistance or decrease vulnerability to invasion (Chapter 2), applying these to on-the-ground management requires more insight into site-specific drivers and relationships. This means taking an empirical approach using field experiments or existing data from the site to actually test which factors are likely driving vulnerability or resistance locally. Given limitations to field data collection at SBDNL in the 2020 season, we used existing

data to address the overarching question: How can invasive species management at SBDNL be informed by measurable ecosystem-level characteristics related to resistance or vulnerability to invasion? We examined the effects of four main variables on vulnerability to invasion at SBDNL: 1) fragmentation, 2) habitat type, 3) native species richness, and 4) herbivore browsing. Before testing these using existing data, we first explain our research rationale and predictions for each variable.

I. Which areas in SBDNL are most vulnerable to invasion due to fragmentation (by development, roads, and trails)?

Current landscapes are increasingly fragmented into small patches of viable habitat surrounded by a matrix of human-transformed land cover (Haddad et al., 2015). Fragmentation increases the amount of edge area and decreases the amount of core, or interior, habitat available to biota (Saunders et al., 1991; Figure 3.1). Current literature indicates that fragmentation is positively related to level of invasion. In managed northern hardwood forests, exotic species have been found to be most prevalent along the edges of unpaved roads and occur less frequently in the interior forest (Gelbard & Belnap, 2003; Hansen & Clevenger, 2005; Mortensen et al., 2009; Watkins et al. 2003). These studies emphasize the ability of invasive species to utilize roads as corridors for expansion, which is of particular concern for large swaths of habitat that are bisected by paved or unpaved roads and developments. Invasive species are most successful when over 20% of the landscape is disturbed by fragmentation; small, isolated patches have higher levels of invasion than larger, connected patches (With, 2004; Vilà & Ibáñez, 2011).

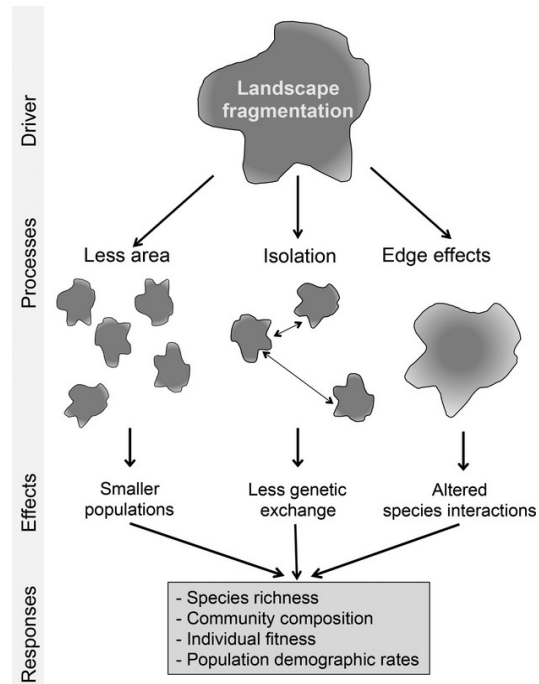


Figure 3.1 | Diagram showing three main effects of fragmentation (reduced size of patches, increased isolation, and increased edge) on plant species and communities (Ibáñez et al., 2014).

We predict that the land around Glen Lake will be more fragmented since many roads and trails are located in this area. As a result, the land surrounding Glen Lake may be a hotspot for invasion. We utilized the software FRAGSTATS to determine which areas are the most likely to be vulnerable to invasion based on fragmentation analyses.

II. How do habitat types in SBDNL differ in the diversity of invasive species?

Research has shown that level of invasion varies across habitat types, which can relate to the factors that increase resistance or vulnerability to invasion (Chapter 2). For example, Vilà et al. (2007) found that habitats that tend to be disturbed, such as riparian habitats, have a higher degree of invasion than habitats that have a lower tendency to be disturbed, like fens and bogs. These findings concur with Chytry et al. (2008), who found that disturbed, human-made habitats had significantly higher proportions of invasive plants. Similarly, Brown and Peet (2003) found that riparian habitats were more invaded than upland areas in terms of invasive species percent cover, frequency, and richness. In this study, we use a long-term vegetation monitoring dataset to test for significant differences in the number of invasive species present between different habitats in SBDNL. These differences may offer insight into habitat-specific vulnerability or resistance to invasion.

III. What is the relationship between native and invasive species richness at SBDNL?

Higher native species richness is thought to increase biotic resistance to invasive species by occupying available niches, but research on the relationship between native species richness and biotic resistance is mixed, leading to the development of the “invasion paradox.” The invasion paradox is the observation that native–exotic richness relationships (NERR) tend to be negative at fine spatial scales and positive at broad spatial scales (Fridley et al., 2004; Peng et al., 2019). According to Fridley et al. (2007), numerous processes affect the relationship between diversity and invasibility. Thus, it may be infeasible to predict whether the NERR will be positive or negative for a given location (Fridley et al. 2007). Although Levine and D'Antonio (1999) agree that both positive and negative relationships occur in NERR, they argue that the relationship is most often positive. Considering the invasion paradox, the tendency for NERR to be positive, and the size of SBDNL, we predict that the number of native species will be positively associated with the number of invasive species when analyzing the park at a coarse scale. Understanding this relationship is important since it will help managers decide

whether to prioritize high or low species rich areas for removal efforts.

IV. What is the relationship between browse and invasive species richness at SBDNL?

Although natural enemies such as herbivores may offer biotic resistance to invasive plants, research also finds that the preference herbivores have for native species can allow for enemy release of the invasive species (Jogesh et al., 2008; Schierenbeck et al., 1994;) and therefore trigger the competitive release and higher success of invasive species (Eschtruth & Battles, 2009). If herbivory increases vulnerability to invasion at SBDNL, we predict that areas with higher observed browse damage will have higher invasive richness. Knowing the relationship between browse damage and invasive species is important for deciding whether or not herbivores need to be considered when creating ecosystem-level resistance-based management plans.

We address these four research questions using two different analytic approaches and data sources. We first address question one by utilizing geospatial data with the programs FRAGSTATS and ESRI ArcMap to identify which areas in SBDNL are more vulnerable to invasion,

based on fragmentation analyses of the protected lands. Then we address questions two, three, and four using the program R to analyze pre-existing data within the park to identify the ecosystem characteristics related to low invasive species resistance. Together, these results have the potential to contribute to the park's proactive approach to manage for resistance to plant invasion by identifying the system-level features related to vulnerability.

Geospatial Analysis: Which areas in SBDNL are most vulnerable to invasion due to fragmentation?

Methods

To identify discrete areas within SBDNL that are vulnerable to plant community invasion, we analyzed existing spatial land use and land cover data using ESRI ArcMap and FRAGSTATS. FRAGSTATS is a spatial pattern analysis program for quantifying the structure (i.e., composition and configuration) of a user-defined landscape (McGarigal, 2015). Analysis can happen at three spatial scales: patch, class, and landscape, and we looked at both patch and class metrics of the landscape. Patch metrics are defined for individual patches, and characterize their spatial character and

context. Class metrics are integrated over all the patches of a given type (McGarigal, 2015). We performed two sets of analyses within the mainland boundary of SBDNL because the mainland has significantly more development than the islands. One analysis reclassified the landscape into undeveloped and developed landscape types to assess fragmentation. The other analysis compared landscape composition at the class level between eight ecosystem types (Table 3.1).

Table 3.1 | Classification of the National Park Service’s Integrated Resource Management Applications categories into groups for fragmentation analysis from Sleeping Bear Dunes National Lakeshore’s management plan.

Ecosystem Type	Map Classes
Bluffs	Great Lakes Beach (erodible sandbank phase) (VES)
Coastal forest (oak, birch, aspen)	Aspen - Birch - Red Maple Forest (FBR), Jack Pine / Blueberry / Feathermoss Forest (FJB), Jack Pine-Northern Pin Oak forest (FJO), Red Pine - Aspen - Birch Forest (FRA), Red Pine / Blueberry Dry Forest (FRP), Spruce - Fir - Aspen Forest (FCP), White Pine - Aspen - Birch Forest (FWA), White Pine / Blueberry Dry-Mesic Forest (FWP), White Pine - Red Oak Forest (FWO)
Dune and shore	Cottonwood Dune Open Woodland (WCD), Eastern Cottonwood Woodland (paper birch variant) (WPB), Great Lake Juniper Dune Shrubland (DJD), Sand Cherry Dune Shrubland (SCW), Great Lakes Beachgrass Dune (HAB), Great Lakes Coast Pine Barrens (barrens phase) (HPB), Interdunal Wetland (HDW), Great Lakes Beach (blowout phase) (VBO)
Developed areas	Developed Area (CDV)
Field	Conifer - Hardwood Ruderal Forest (FMX), Conifer Ruderal Forest (FCX), Deciduous Orchard (FOD), Hardwood Ruderal Forest (black locust phase) (FBX), Hardwood Ruderal Forest (hardwood mix phase) (FDX), Conifer - Deciduous Ruderal Shrubland (SMX), Conifer Ruderal Shrubland (SCX), Deciduous Ruderal Shrubland (SDX), Ruderal Grassland (HMX), Bracken Grassland (HBF), Crop Field (HCF), Pasture Field (HPF)
Northern Conifers (white and red pine, cedar)	Conifer Plantation (FPE), Great Lakes Dune Pine Forest (FPD), Great Lakes Coast Pine Barrens (woodland phase) (HPW)
Northern hardwoods (maple, beech, ash)	Beech- Maple- Northern Hardwood Forest (FBM), Great Lakes Hemlock - Beech - Hardwood forest (FHB), Northern Red Oak - Sugar Maple Forest (FOM), Sugar Maple - Ash - Basswood Northern Rich Mesic Forest (FMA), White - Cedar - Boreal conifer mesic forest (maple coastal dune phase) (FCM)
Wetlands	Black- Ash- Mixed Hardwood Swamp (FBA), Black Spruce - Tamarack / Labrador tea Poor Swamp (black spruce phase) (FSS), Black Spruce - Tamarack / Labrador tea Poor Swamp (tamarack phase) (FTP), Central Tamarack Poor Swamp (FTS), Hemlock Mesic Forest (FHC), Hemlock - Yellow Birch Swamp Wet-Mesic Forest (FHS), Northern Tamarack Rich Swamp (FTR), Red Maple - Ash - Birch Swamp Forest (FRM), White - Cedar - (Mixed Conifer) / Alder Swamp (FCS), White-cedar - Black Ash Swamp (FCA), White - Cedar - Boreal conifer mesic forest (conifer phase)(FCC), White - Cedar - Boreal conifer mesic forest (yellow birch interior phase) (FCB), White Pine- Red Maple Swamp (FWS), Dogwood - Willow Swamp (black chokecherry phase) (SBC), Dogwood - Willow Swamp (dogwood - willow phase) (SDW), Gray Alder Swamp (SAS), Leatherleaf Poor Fen (DLF), Leatherleaf - Sweetgale Shore Fen (DLS), Shrubby-cinquefoil - Sweetgale Rich Shore Fen (SSF), Bluejoint Wet Meadow (HCC), Eastern Reed Marsh (HPG), Great Lakes Sedge Rich Shore Fen (HSM), Inland Coastal Plain Marsh (HCP), Midwest Mixed Emergent Deep Marsh (HCM), Midwest Pondweed Submerged Aquatic Wetland (HSV), Northern Great Lakes Emergent Marsh (HEM), Northern Sedge Wet Meadow (HSG), Northern Water-lily Aquatic Wetland (HFA), Upright Sedge Wet Meadow (HUS), Wet Meadow Mixed Herbaceous (HWM), Woolly-fruit Sedge Shore Fen (HSS)

For all geospatial analyses, we utilized existing vegetation mapping data from the National Park Service's Integrated Resource Management Applications (IRMA) for SBDNL, which also includes roads, buildings, campgrounds, and parking lots. Geospatial data of park trails and roads are from the National Park Service open source data portal (The National Park Service, n.d.). All data were originally in or projected to the NAD 1983 datum and UTM Zone 16N projection.

The IRMA vegetation map data was simplified into fewer habitat categories (Table 3.1) for class-level analyses because the number of discrete classes in the original would have limited the usefulness of a patch analysis in FRAGSTATS. Broader habitat categories are based on a natural resources map from the SBDNL's 2009 General Management Plan/Wilderness Study Summary; they include bluffs, coastal forests, dune and shore lands, fields, northern conifers, northern hardwoods, wetlands, and developed areas (roads, trails, parking lots, campsites, and buildings) (Figure 3.2). Classifying our own map output allowed for finer scale classification compared to the map in the General Management Plan. The reclassified vegetation types exclude a few IRMA vegetation map categories to keep with the

project's primary focus on terrestrial invasive plants; the excluded categories, such as water bodies, cannot contain terrestrial invasive plants. The simplified vegetation map is shown in Figure 3.3.

For the undeveloped vs. developed landscape analyses, we merged the ecosystems into one "undeveloped land" category. This undeveloped category includes the categories excluded for the class analysis (e.g., water bodies). Developed land was classified as land containing roads, campgrounds, buildings, parking lots, etc.

After reclassifying our data, we merged polygons of the same classification and rasterized the map for analysis. Cell raster size was set to 2.5 meters to meet FRAGSTATS requirements that cell size not be less than 1/2 of the narrowest patch dimension (McGarigal, 2015). The smallest dimension we found when examining the map was approximately 5 meters. To prepare the raster for importing into FRAGSTATS, we assigned all vegetation types arbitrary values (Table 3.2) and created a border around the park boundary with negative values. These values are utilized by FRAGSTATS with the moving window to compute metrics for cells along the border. The seven metrics we chose to analyze in FRAGSTATS are listed in Table 3.3,

and include tests at the patch and class levels.

In a separate raster, we reclassified all land cover types as developed or undeveloped areas to assess landscape fragmentation by development. This raster file was used in FRAGSTATS with patch metrics (AREA and SHAPE) to analyze where human influence has the greatest impact in the landscape. AREA ranks patches according to total area, and SHAPE analyzes patches according to shape irregularity, which is a metric for edge assessment. Our FRAGSTATS results were then loaded back into ArcMap for spatial analysis.

After spatially orienting our results, we used the raster calculator to overlay the metrics to see which patches had both the lowest area and highest shape irregularity (Appendix B). We equally weighted the values of both metrics to visualize which patches of natural land were the most fragmented by roads, buildings, and trails irrespective of vegetation type. Finally, we reclassified the combined values using Jenks Natural Breaks to simplify the scale of fragmentation from low to high, for easier communication of the results in a color-coded map depicting the level of fragmentation (Figures 3.4 & 3.5).

We created two maps, one including both trails and roads within the park boundary (Figure 3.4) and one excluding trails (Figure 3.5). Trails have less motor vehicle activity and are smaller – two possible reasons that trails could be less vulnerable to invasion. Lundgren et al. (2004) observed that richness and cover of invasive species in a Connecticut forest were significantly greater along paved roads than along trails. Additionally, they found that invasive richness, cover, and frequency increased with expanding road size. We recommend considering both maps to inform management decisions.

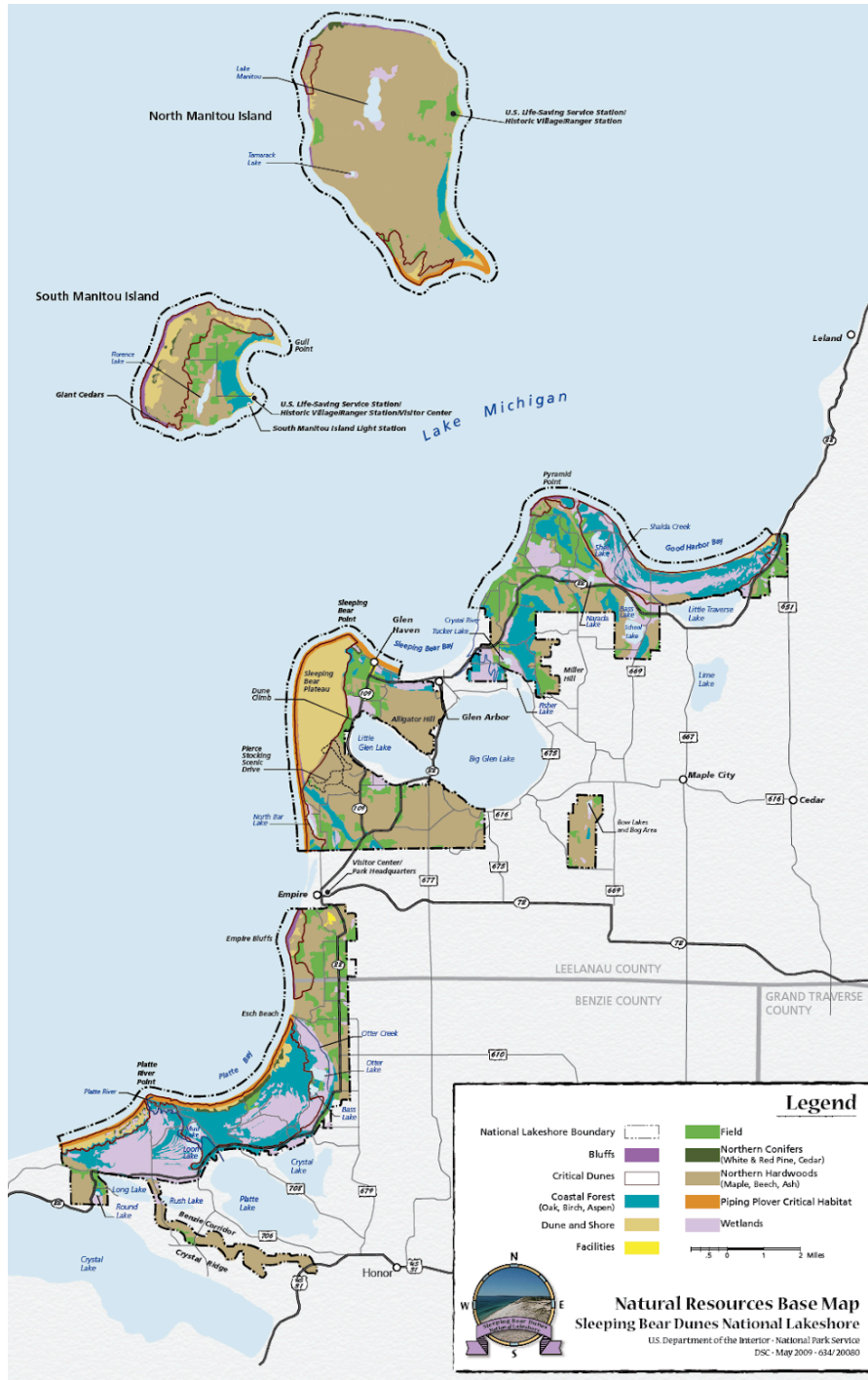


Figure 3.2 | Resource classification map from Sleeping Bear Dunes National Lakeshore's management plan (Sleeping Bear Dunes National Lakeshore, 2009).

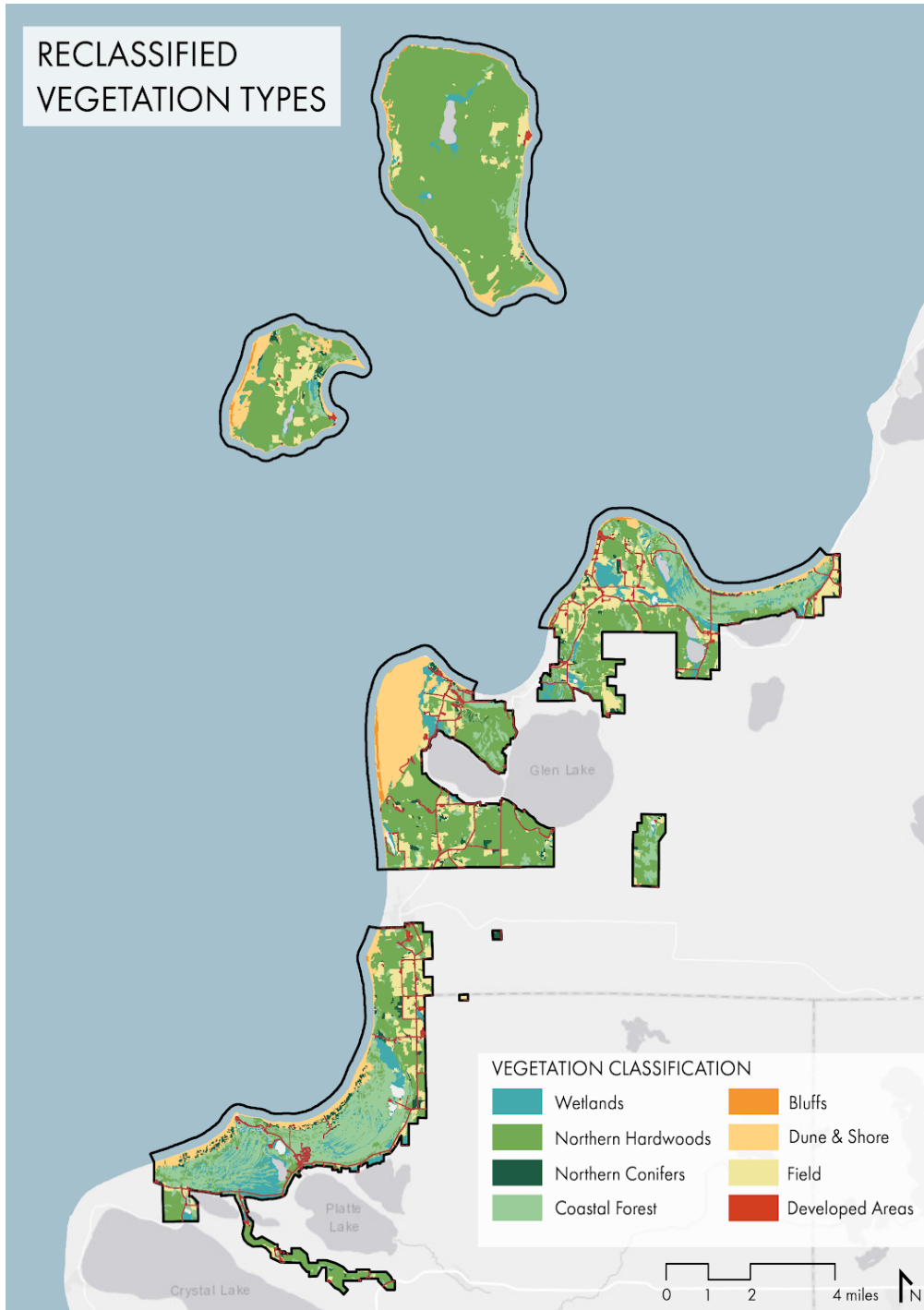


Figure 3.3 | Final ecosystem classification map for fragmentation analysis. Includes land within the project boundary from Integrated Resource Management Applications (IRMA).

Table 3.2 | Classification values for the different land cover types from the SBDNL management plan map.

Map Class	Value
Developed areas (CDV)	1
Coastal forest (FBR)	2
Dune and shore (DJD)	3
Bluffs (VES)	4
Field (FBX)	5
Northern conifers (FPE)	6
Northern hardwoods (FBM)	7

Table 3.3 | Description of chosen FRAGSTATS metrics for analysis.

Level	Metric	Description
Patch	AREA	Gives the area of each patch. Utilized in developed vs. undeveloped analysis.
Patch	SHAPE	Measures the complexity of patch shape compared to a standard shape (square) of the same size. Utilized in developed vs. undeveloped analysis.
Class	Total area	How much of the landscape consists of a particular patch type (area).
Class	PLAND	How much of the landscape consists of a particular patch type (percentage).
Class	AREA_MN	Mean area of the patches in a certain class.

Results & Discussion

I. Fragmentation analysis

Human developments within the park, including roads, buildings, campsites, parking lots, and trails, varyingly fragment the natural landscape across the park.

Combining the SHAPE and AREA indexes, (Appendix B), reveals that the most fragmented lands are those with irregular shape and small area; they are indicated in red and orange in Figures 3.4 and 3.5.

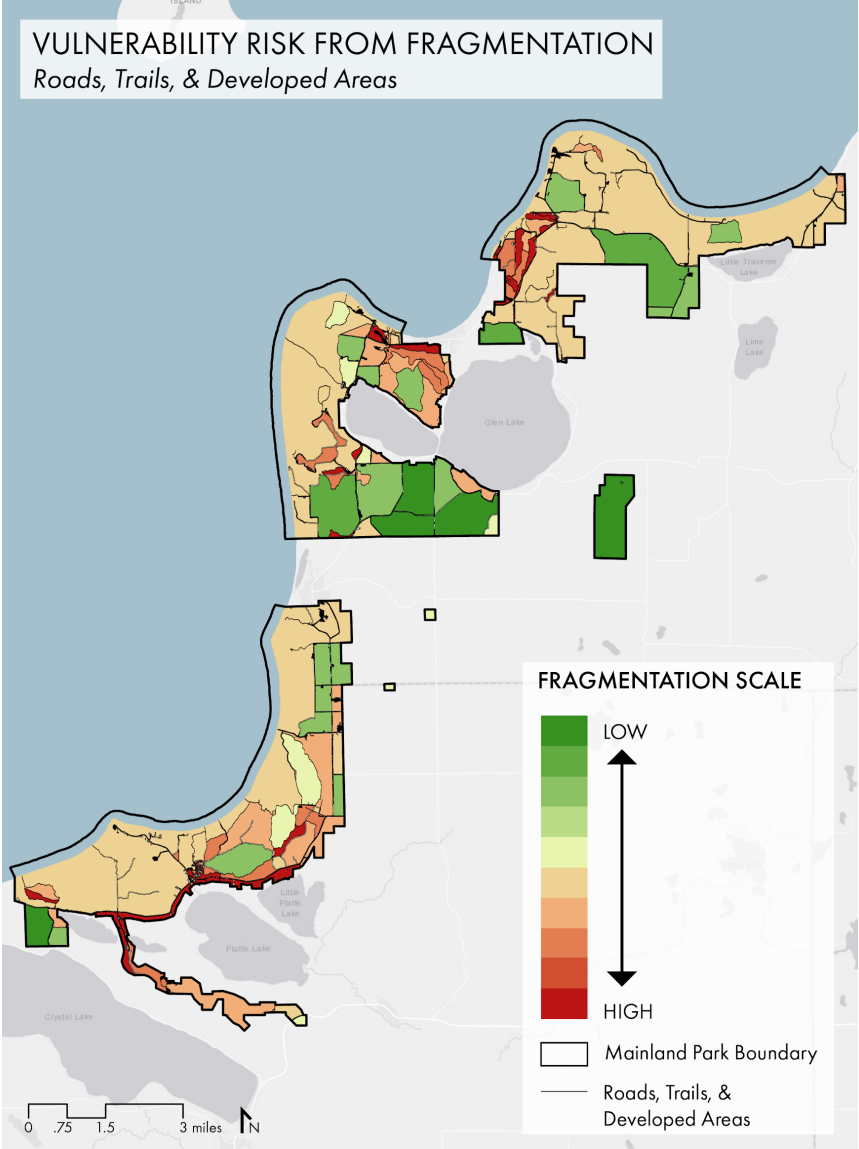


Figure 3.4 | Map of land parcels within park boundaries fragmented by all development. Shown on a scale from least to most fragmented in green to red.

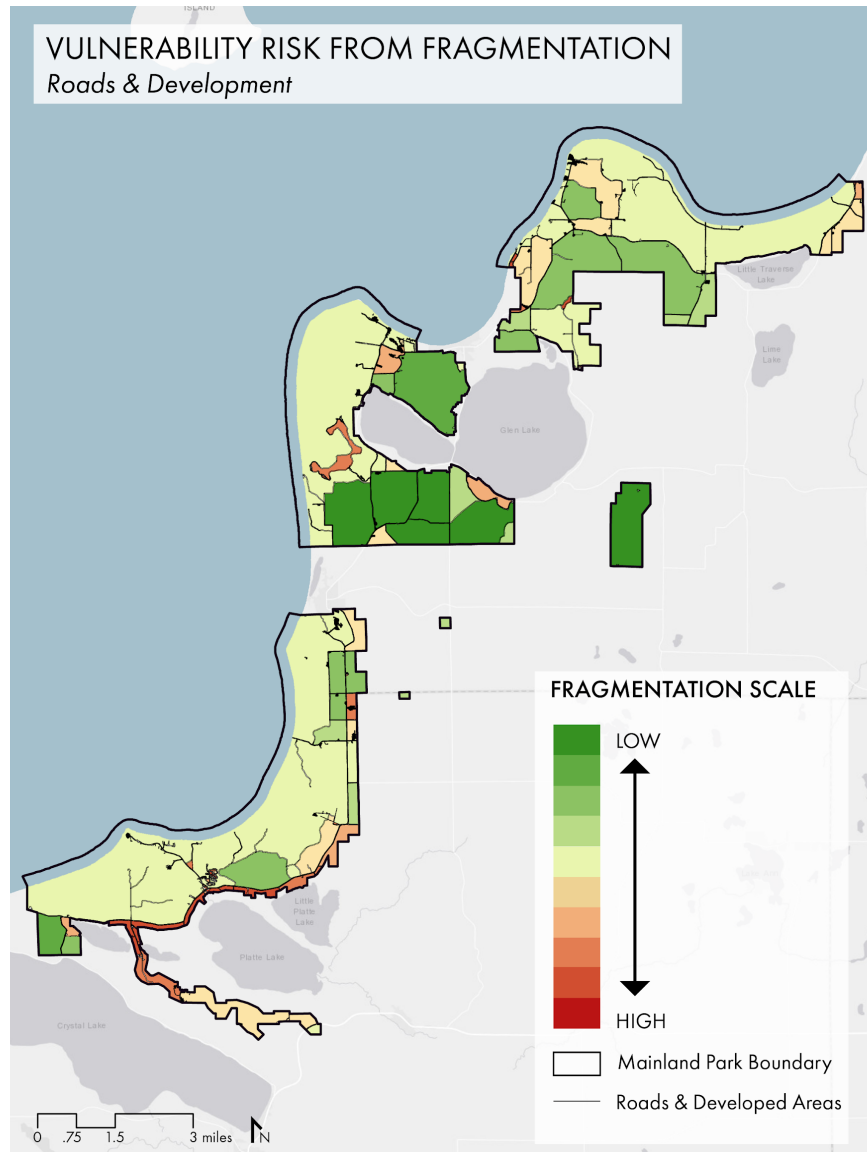


Figure 3.5 | Map of land parcels within Sleeping Bear Dunes National Lakeshore (SBDNL) boundaries fragmented by roads and development, excluding trails. Shown on a scale from least to most fragmented in green to red.

Three major areas of high risk to invasive species emerge from the fragmentation analysis when roads, trails, and other developed areas are considered. The first area is the section of the park located in Benzie Corridor. The parklands in Benzie Corridor were initially established to

create a scenic roadway (Great Lakes Invasive Plant Management Team, 2020). However, the National Parks Service (NPS) has not yet acquired enough land to construct the roadway. NPS owns about 100 acres, or about 10% of Benzie Corridor (Great Lakes Invasive Plant Management

Team, 2020). The land that NPS currently owns on Benzie Corridor is narrow and long, which creates a high amount of edge. If the land beyond the park's boundary is developed, it will create a high degree of fragmentation in this area of SBDNL, which may further fragment this land. It is important to note that construction of the scenic roadway is likely to increase fragmentation. With these considerations in mind, we support NPS's decision to continue acquiring land before building the scenic roadway. Owning more land on Benzie Corridor may reduce the effect of adding a road, since a lower percentage of the park-owned corridor will be road. Acquiring more land on the corridor may also decrease the amount of edge in this area of SBDNL. In the meantime, NPS should prioritize their land in Benzie Corridor for monitoring and resistance-based management practices.

The second area that is highly threatened by invasive species due to fragmentation extends northward from Benzie Corridor to the land that is in between the Michigan-22 highway (M-22) and Platte and Little Platte Lakes. Similar to the part of SBDNL that lies within Benzie Corridor, the land that lies between M-22 and Platte and Little Platte Lakes is long and narrow, which creates a high amount of edge. This land borders M-22 on one side

and developed lakefront properties on the other. As a result, this land is highly fragmented and may be highly vulnerable to invasion. This area should also be prioritized for monitoring and resistance-based management practices.

Park lands surrounding Glen Arbor form the third area that has a high risk for invasive species due to fragmentation. The highly fragmented areas are towards the beachfront rather than inland (Figure 3.4). This area of land is not considered highly fragmented when the model is run without trails (Figure 3.5). The difference between the two model outputs indicates that beachfront trails are the main cause of fragmentation in the Glen Arbor area. The areas directly north and south of Glen Arbor are thus where we recommend prioritizing monitoring and resistance-based management practices.

II. Landscape Class Analyses

We used class metrics in FRAGSTATS to determine the percent cover of each vegetation type in the park and their average patch size (Figure 3.6). Comparing the class percentages to the mean patch size provides greater insight into landscape composition than viewing each metric alone. For a given class, a larger mean patch size relative to percentage indicates that the

class is subdivided into larger parcels and experiences less fragmentation by developed areas. Land cover types Dune & Shore and Bluffs have large mean patch sizes relative to their total percentage in the landscape. In contrast, Northern Hardwoods and Coastal Forest land cover types together comprise the majority of the land cover in Sleeping Bear yet have smaller mean patch sizes than Dune & Shore and Bluffs. Fragmentation may be greater surrounding and within these patches, resulting in smaller mean patch sizes. The Field category is also relatively fragmented

according to these calculations. We recommend preventing further fragmentation of the Northern Hardwoods and Coastal Forest classes, as they may be at higher risk for invasion due to small mean patch size relative to the percent cover of landscape. More rare classes, such as Northern Conifer forest and Wetlands, also have small mean patch sizes and therefore should be prioritized for resistance-based management both because of their rarity and increased vulnerability to invasion.

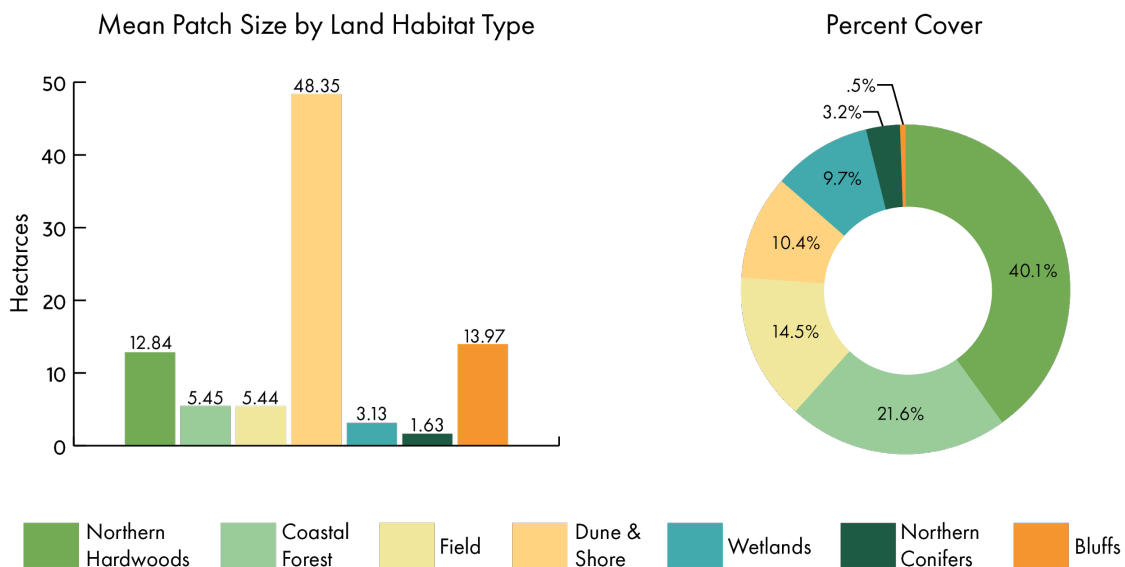


Figure 3.6 | Percent land cover and mean area of patches for each ecosystem classification.

Analysis of vegetation monitoring data: How are habitat, native species richness, and browse related to vulnerability to invasives?

Methods

To test the relationship between select variables and vulnerability to plant invasion, we used existing vegetation and habitat information from the Great Lakes Inventory and Monitoring Network (GLKN) – a large-scale vegetation monitoring dataset that includes data from 2018 in SBDNL. Data are collected in 50 x 100 meter plots in forested areas with three, 50-meter transects. Each transect has ten, one-meter squared quadrats located five meters apart (Sanders & Grochowski, 2014). Within the quadrats, all native and invasive plant species were identified and recorded as being present. We also had access to walkthrough data from the park, where additional invasive species were noted at the larger plot rather than quadrat level. Habitat type was classified at the plot level as well. In order to include both the quadrat and walkthrough data, we conducted our analyses at the plot level. In addition, data on browse damage of plants by large herbivores were collected in 68, one-meter radius (3.14 m²) circles equally spaced along seven, 50m transects

in each plot (Sanders & Grochowski, 2014). Presence of browse was recorded for each identified plant species, and per plot totals were calculated as the number of species that had a direct browse occurrence.

From all of the variables measured in the GLKN dataset, we chose three that had the potential to affect community resistance or vulnerability to invasion: habitat type, native species richness, and browse damage. For each we tested for a significant relationship with the level of invasion, which was measured as the number of invasive plant species recorded in the same plot (abundance data was not available).

For each variable of interest, we aggregated counts from the GLKN dataset and the walkthrough dataset at the plot level. Using these aggregated data, we ran a generalized linear model (GLM) with a Poisson distribution, which is best suited for count data (Ridout et al. 1998), in R. Poisson distributions are based on log links, so we exponentiated the linear predictors in the results. Then for all habitat types, aside from Balsam/mixed conifer (our intercept), we subtracted the exponentiated value from one to obtain the percent increase in invasive species for the Balsam/mixed conifer habitat type, compared to the habitat type of interest. For the Native variable, we subtracted one from the

exponentiated estimate to find the rate of increase/slope in invasive species as it relates to the number of native species. Prior to running the model, we checked for multicollinearity with the *vif()* function. We created a marginal effects model in R for evaluating native versus invasive species diversity because the relationship is significant and linear. The marginal effects model computes predicted values from the best fit line with a 95% confidence interval.

Results & Discussion

Invasive species count (our measure of vulnerability) was significantly related to habitat type and native species richness but not browse, according to the results of our generalized linear model (Table 3.4). Comparing habitat types, both pine and sugar maple/beech habitats had significantly lower numbers of invasive species than Balsam/mixed conifer habitats, which had over 60% higher invasive diversity (Figure 3.7).

Table 3.4 | Output of the generalized linear model. The intercept for habitat type is Balsam/mixed conifer, so it is not included. The habitats listed are in comparison to the intercept.

Variable	Estimate	Estimate (exponentiated)	P-value
Habitat Type			
Balsam/mixed conifer	-0.316	0.729	0.469
Pine	-0.959	0.383	0.014 *
Red maple / beech / mixed hardwood	0.656	0.519	0.053
Sugar maple / beech	-1.021	0.360	2.92e-05 ***
Native Species Richness	0.041	1.042	1.26e-05 ***
Browse damage (count per plot)	0.019	1.019	0.062

Native species richness was associated with an increase in invasive richness. For every one species increase in native species, the probability of an increase of one species of invasive increases by 4.23% (Figure 3.8). This indicates that the invasion paradox may be observable at SBDNL. To further understand whether the invasion paradox is occurring, future studies should analyze the relationship between native and invasive species at SBDNL at finer scales.

The amount of browse was not significantly related to invasive species richness. An insignificant result does not necessarily mean that there is no relationship, especially considering that the p-value was nearly significant at 0.0622. It may be that invasive abundance of certain species is more affected by browse than species richness, an area that deserves more research with a larger sample size.

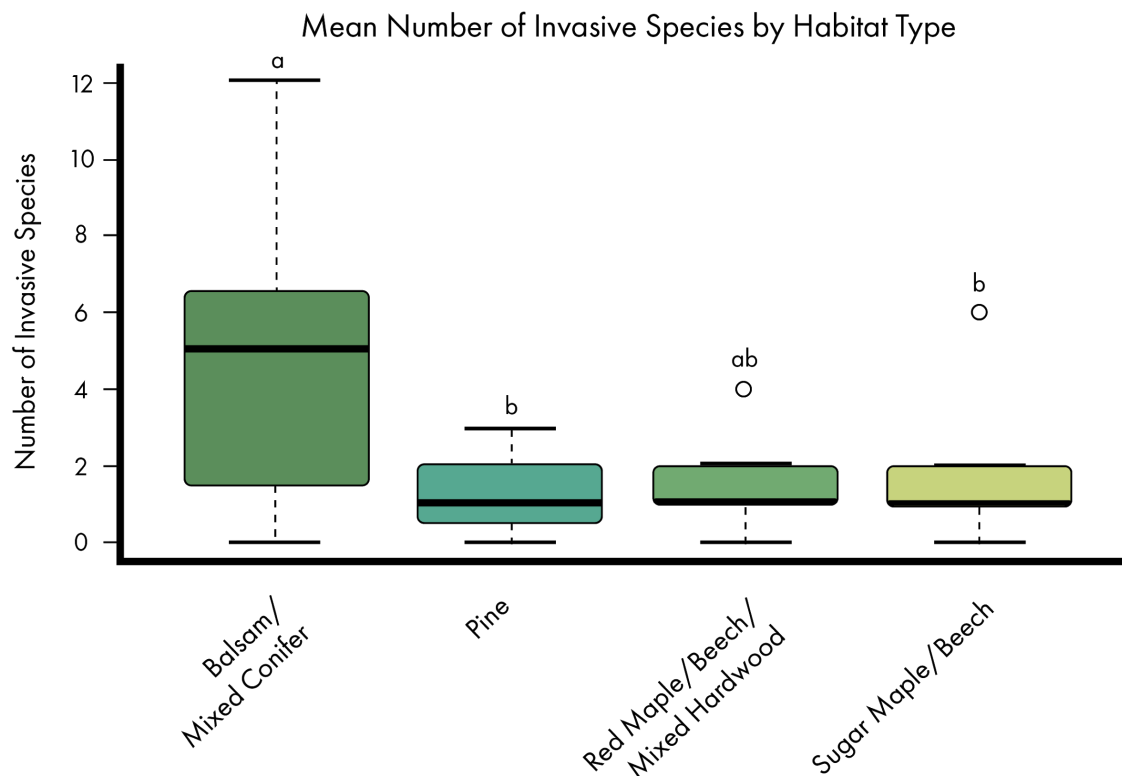


Figure 3.7 | Boxplot showing the number of invasive species per plot based on the habitat type. Pine and Sugar Maple/Beech both contain significantly fewer invasive species than Balsam/Mixed Conifer.

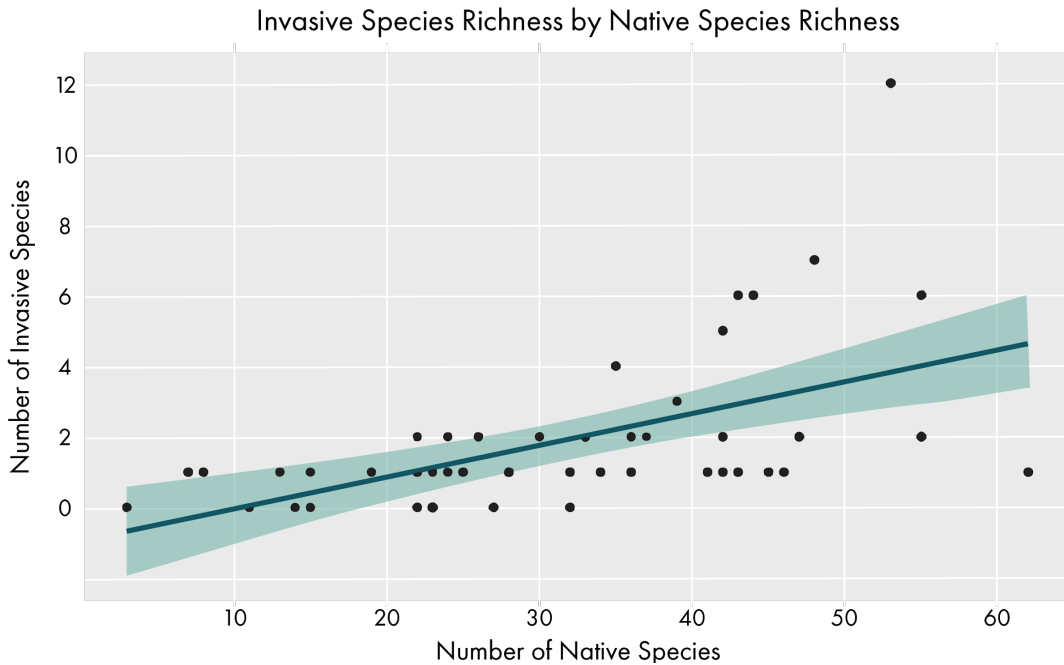


Figure 3.8 | Scatter plot of the number of invasive species per plot against the number of native species per plot with a best fit line and marginal effects shown.

Conclusions & Recommendations

While our analyses are limited by available data, they provide insight into next steps for research and management of invasive plants at SBDNL. Our analyses relied upon existing GLKN data that were collected for a long-term, comprehensive monitoring program designed to detect forest changes over time and to monitor forest health (GLKN, 2014). Since this dataset was not designed to test relationships between ecosystem characteristics and resistance to invasion, valuable variables are missing. In the future, the long-term monitoring data could be tailored to collect variables that can help

identify ecosystem vulnerability to invasive species. Specifically, we recommend adding measures of propagule pressure, resource availability, and/or functional group diversity to the long-term monitoring data. Propagule pressure is believed to have a strong, positive relationship with invasion (Eschtruth & Battles, 2009) and can be measured using methodologies such as those used by Eschtruth and Battles (2011). Changes in resource availability and use can be measured by testing soil for its moisture content, pH, total nitrogen, and total carbon (Kuebbing et al., 2013). Availability of light and space are also important resources to measure and can be assessed as canopy

cover (using an available app) and percent bare ground. Functional group richness is also important to measure, as it can increase resistance to invasion due to complete niche occupation of resources (Chapter 2). Functional diversity can be monitored using available plant inventories and known functional characteristics by species.

Analysis of existing GLKN data did reveal differences in vulnerability by habitat but did not support a strong impact of native diversity or browse damage on vulnerability, again highlighting priorities for future research. We recommend that Balsam mixed-conifer forests, which have significantly higher invasive species richness than pine and sugar maple/beech forests, should be monitored and possibly treated to improve native functional diversity. The high level of invasive diversity suggests that there may be a lack of biotic resistance in this habitat, and native seeding, with species in the same functional groups as the invasives present or with more competitive native species, could reduce invasive presence in this habitat.

Since our analysis is confined to inland forest ecosystems, future research should prioritize collecting data in other ecosystems, particularly dunes and coastal environments, to get a more complete

picture of how vulnerability varies across ecosystem types. Further data collection would also be useful for forests affected by the emerald ash borer (*Agrilus planipennis*), where the loss of ash trees is creating available resources for potential invaders. SBDNL has already expressed a desire to establish long-term compositional and structural complexity in forests affected by the emerald ash borer, so these forests would be ideal for studying the impact of actively managing for resistance by increasing plant cover or diversity.

A finer-scale analysis would provide a more comprehensive understanding of key variables affecting ecosystem resistance to invasive species, which would in turn allow for more specific management recommendations tailored to different areas. In addition, the data collection methods prevented us from using individual count data, so our analysis tested variables against invasive species richness only. A more effective measure would use individual count data to calculate and analyze the Shannon's diversity index of plots as the dependent variable.

Our fragmentation analysis identified three major sites in SBDNL to prioritize for management and monitoring: Benzie Corridor, the land between M-22 and Platte and Little Platte lakes, and the beachfront

trails near Glen Arbor. For the parcels that border private lands, such as the land between M-22 and Platte and Little Platte lakes, we recommend outreach and education for private landowners that border the area. This approach to assessing and responding to vulnerability can be built upon in the future by including the above-mentioned additional variables to refine output maps and more accurately predict vulnerable areas. This approach can subsequently be tested using field measures of invasive diversity and abundance. In addition, we chose to recategorize the more specific land cover types into eight broader categories defined by SBDNL (Table 3.1). While this was necessary for an effective analysis, the vegetation boundaries between the two maps were not always clear, particularly for the wetland and coastal forest categories. Ground-truthing these ecosystem extents is advised for a more accurate analysis.

Site-specific testing of ecosystem characteristics that may influence community resistance and vulnerability to invasion is essential for informed management. Drivers of invasion vulnerability and resistance are very likely to vary by ecosystem and even site history. We recommend that SBDNL and other sites managing for invasive plant species

continue to take an adaptive management approach where management actions are treated as controlled field experiments. Doing so will inform future management in a manner that builds ecosystems that are more resistant to the impact of invasions in the long term.

Chapter 4 | Lessons from Practice

What is associated with vulnerability, and what are the successes and barriers of resistance-based management?



Bethany Louria, 2020

Based on current research in invasive species management (Chapter 2), we know that there are limitations with current single-species attempts to manage invasives. We also identify theoretical and empirical evidence for characteristics that make communities more or less vulnerable to invasive plants that could be used to inform a more systems-based approach to management. While this theory and

empirical results are useful, they do not tell us what practitioners are actually doing and experiencing on the ground. That is, what do they see as the characteristics that cause vulnerability and resistance, and how can or do they integrate these into their practices?

One of the primary issues we explore in this chapter is the possible disconnect between invasive species research and actual on the ground perspectives and

management practices. In a review of current literature, Esler et. al (2010) reveal a lack of research that focuses on the actual implementation of invasive species management practices (“doing”); instead, the focus is on continuing to build the general knowledge base (“knowing”). They refer to this disconnect between research activities and what is needed or even done in practice as the “knowing-doing gap.” In order to address this gap, we discuss the perspectives of practitioners on current management practices, the qualities they use to define vulnerable communities, and their perceived barriers to implementing systems-based management approaches. Our goal in hearing the perspectives of practitioners is to challenge the assumption that only research supports management. A two-way flow of information between research and management is crucial to the implementation of effective invasive species management.

To gain this management perspective, we engaged with practitioners in two main settings. We facilitated an interactive workshop for Great Lakes region practitioners on shifting the framing of invasive species management from species to community characteristics (Figure 4.1), and we conducted individual interviews with a variety of different land managers to gain

a more in-depth perspective on the specific needs and realities of a resistance-based approach to invasive species management. The workshop was an opportunity for managers to share their knowledge and experiences with us and each other. It also promoted valuable group discussion on invasive plant management practices, characteristics of vulnerable and resistant sites, and barriers to managing invasive plants. The interviews further helped us understand the needs and realities of invasive plant management from the perspective of the practitioner and expanded on the questions discussed at the workshop.



Figure 4.1 | Practitioners attending the “Reframing Invasions” workshop.

Specifically, we addressed the following research questions:

1. What characteristics do practitioners associate with more vulnerable or more resistant plant communities?
2. In what ways do practitioners take a systems-based approach (vs. treating single species) to reduce invasive presence or impact? What are the lessons they have learned?
3. What are the challenges or barriers to adopting resistance-based approaches? How do practitioner decision-making processes and structures (goal- and priority setting, funding, and planning cycles, etc.) affect their ability to implement a systems-based approach?

Methods

I. Practitioner workshop discussions

On February 28th, 2020, faculty from the University of Michigan's School for Environment and Sustainability co-led a workshop titled "Reframing Invasions: From the Invader to the Invaded" in Ann Arbor, MI. Approximately 60 practitioners from a variety of organizations across the state attended this workshop (Table 4.1).

Table 4.1 | List of organizations represented at the workshop on February 28th, 2020.

Ann Arbor Wild Ones
City of Ann Arbor Natural Areas Preservation
Feral Flora
Friends of Rouge Park
Huron-Clinton Metroparks
Inter-Tribal Council of Michigan
Matthaei Botanical Gardens & Nichols Arboretum
Michigan Department of Agriculture and Rural Development
Michigan Department of Natural Resources (DNR)
Michigan DNR- Parks & Recreation
Michigan DNR- Wildlife Division
Michigan Natural Features Inventory
Michigan Nature Association
Michigan State University
Michigan Technological University
National Park Service- Indiana Dunes National Park
The Nature Conservancy
NatureWrite LLC
Northwest Michigan Invasive Species Network
Purdue University
Sault Ste. Marie Tribe of Chippewa Indians
Stiltgrass Working Groups
United States Geological Survey
University of Michigan- School for Environment & Sustainability
Washtenaw County Parks & Recreation

The workshop agenda was designed to engage attendees in discussions about a variety of topics related to invasive plant management in terrestrial systems, with a particular emphasis on vulnerability and resistance concepts and approaches.

Facilitators at each table captured notes during discussion sessions and joint ideas were captured in flip charts (Figure 4.2). The main topics covered in workshop discussions were about the challenges and lessons of invasive plant management, the responses to meta-analysis results (Ibáñez

et al., 2021), and priorities for next steps (Table 4.2). Here, we discuss only those discussion topics that related directly to our three main research questions posed above.

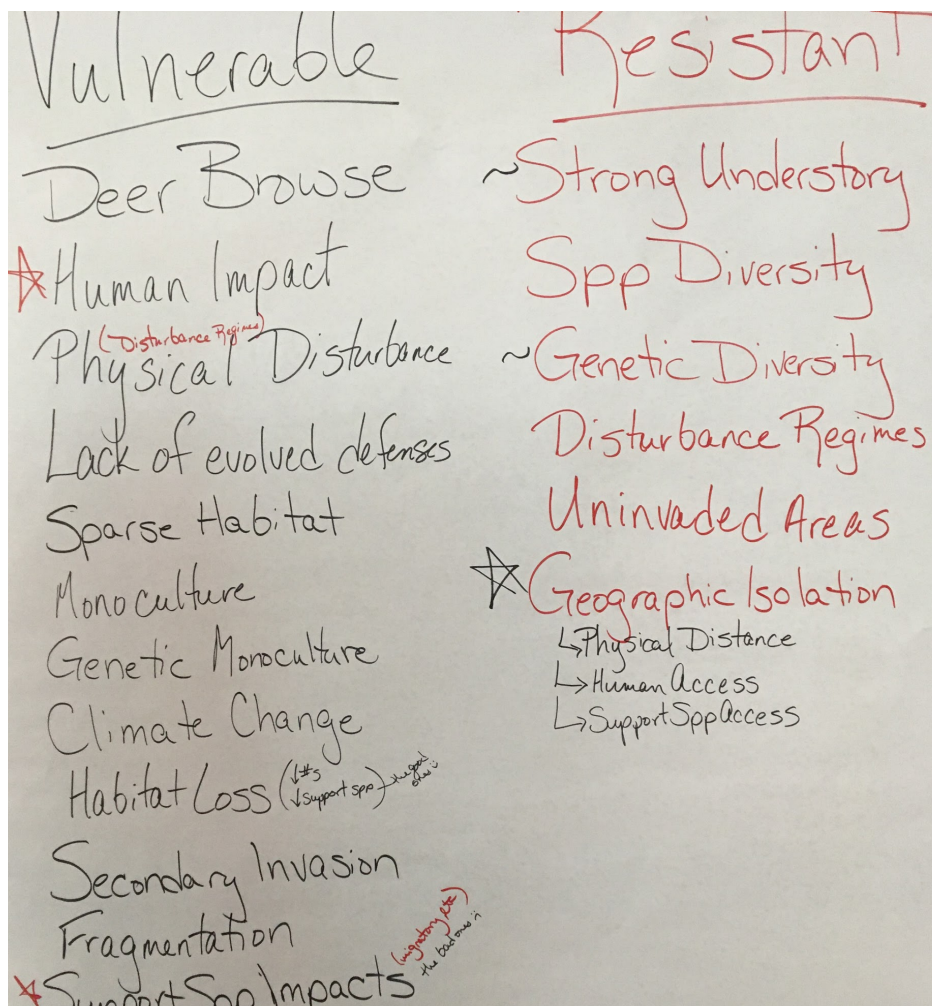


Figure 4.2 | Example of report-out notes from one group in the workshop discussion on the characteristics practitioners see as causing community vulnerability or resistance to invasive plants.

Table 4.2 | Main topics and example discussion questions from the workshop.

Challenges and lessons of invasive species management from practice:
1. What does the success or failure of invasive species management have to do with the community?
2. What do you think makes a plant community vulnerable to invasions (general and specific features)? What makes it resistant?
3. Which community features are you most vs. least certain about in terms of how they affect invasion?
Response to meta-analysis of the factors that related to resistance and vulnerability:
1. Were any of the results surprising to you?
2. Are there other/related mechanisms or metrics of resistance not covered in the results that you think should be used?
3. In your experience, when and what types of disturbance increase vulnerability to invasion vs. what types facilitate the native community/prevent invasion? What do you need to know about a site to use disturbance effectively in management?
Priorities for next steps:
1. What site-specific or general data, reviews, analyses, or tools do you most need to more effectively manage for resistance or resilience?
2. What institutional, funding structure, or social barriers do you face to implement resilience-based management?

II. In-depth interviews

In addition to gathering perspectives at the workshop, we subsequently conducted eight approximately one-hour structured phone interviews with a variety of practitioners from the Great Lakes region. Approximately 60 of these practitioners also attended the workshop. Interviewees were selected based on their involvement with terrestrial plant communities and invasive species management and had mid-level field experience or were managers overseeing field activities. Their positions included invasive plant project manager, director of natural areas and preserves, stewardship coordinator, stewardship specialist, project manager in restoration, and chief of natural resources. Our goal in conducting these interviews was to gather information that specifically addressed our research questions and to gain more in-depth and individual perspectives from practitioners currently working on the ground. Interview questions were formulated to help us better understand the current approaches practitioners employ with their respective organizations, how they incorporate systems-based approaches, and what resistance-based practices mean to them. The specific questions we asked are listed in Table 4.3,

and a complete interview guide can be found in Appendix C.

To analyze the information we gathered, we anonymized all observational data compiled from the "Reframing Invasions" workshop and from our interviewee identities. When discussing our results, we reference all vulnerability and resistance characteristics as originally framed by practitioners.

Table 4.3 | Topics and sample questions asked in structured interviews of practitioners.

Interview Guide Topics	Sample questions asked
Background on ecosystem type and observed disturbances	<ul style="list-style-type: none"> • Which of the ecosystems or sites that you manage are most <i>vulnerable</i> to invasives (that is, have the highest rates of invasion)? • What disturbances are you seeing? What do you consider to be a disturbance?
Current management approaches and prioritization	<ul style="list-style-type: none"> • What are the most common tools/approaches you use to control invasive species presence or impact in these ecosystems? • In what ways have you taken a systems-based approach (vs. treating single species) to reduce invasive presence or impact?
Barriers on employing system-based approaches	<ul style="list-style-type: none"> • What do you think are the biggest challenges or barriers to taking a systems-based approach to invasive species management? [First asked open-ended before prompting each of the topics below.] <ul style="list-style-type: none"> ○ Capacity? - funding, labor, time ○ Institutional barriers? ○ Public perceptions?
Decision-making in invasive plant management and what informs practitioner decision-making	<ul style="list-style-type: none"> • What are barriers to applying new ways of managing invasives? • What would facilitate applying alternative approaches? • Do you use adaptive management? • Given the processes for decision-making, how can we best integrate our recommendations/new approaches?
Future of invasive plant management/expectations	<ul style="list-style-type: none"> • Given continued invasions, climate change, and other stressors, what do you see as needed in the future of invasive species management?

Results & Discussion

I. What characteristics do practitioners associate with more vulnerable or resistant plant communities?

Disturbance

Natural disturbance regimes, when at appropriate levels, are viewed as increasing resistance to plant invasion. Practitioners describe how altered or missing disturbance regimes increase site vulnerability and recognize that intact systems with a lack of historic disturbances and development are more resistant. Intact natural processes, such as fire and hydrological cycles, are identified as supporting community resistance, but earlier stages of succession, even after natural disturbance, are seen as more vulnerable to invasion. Disturbances that are outside of the range of natural variability are recognized as problematic. For example, herbivory by overabundant deer is viewed as increasing vulnerability, and the absence of that excessive herbivory as increasing resistance. Similarly, the novel and intense disturbances associated with climate change, including shifting and novel pests and diseases, are seen as increasing vulnerability.

Practitioners recognize that anthropogenic disturbances, such as

development, agricultural activities, or visitor usage and associated development, are associated with vulnerability – especially at intensely disturbed sites. They also observe that management can be a form of disturbance, especially in relation to the potential for secondary invasions that can follow post-treatment. This dynamic is confirmed by the literature on secondary invasions (Chapter 2) and the documented relationship between anthropogenic disturbances, including management, and invasive performance (Ibáñez et al., 2021). For example, practitioners share how invasive treatments at low-quality sites are not necessarily very effective because the sites often do not recover well, and management creates an “herbicide or disturbance scar.” These scars take time to heal, and undesirable vegetation often moves in to fill these openings via secondary invasion. Thus, practitioners express a desire to choose sites and management techniques that reduce unintended impacts.

Practitioners observed that decreases in habitat and buffers and increases in fragmentation and edge effects increase the likelihood of invasion. This aligns with research showing that fragmentation alters landscape configuration and is oftentimes related to the arrival and establishment

phases of an invasion (Vila and Ibáñez, 2011). Practitioners recognize that increased site connectivity, described as “proximity to the matrix,” is a characteristic of resistant plant communities. Another practitioner highlights the importance of connectivity for the stability of ecosystems:

“All these things could create these little ***niche environments that could make the migration of plants and animals more resilient over time.*** Within these areas, there’s a lot of diversity for the animals and plants to adapt over time.”

Abiotic Factors

Practitioners have mixed perspectives on the relationship between extreme physical conditions and vulnerability. In general, they note that communities with abiotic extremes are more resistant as a factor of nutrient availability, soil chemistry, hydrology, or soil moisture. The role of nutrient extremes is less straightforward given that practitioners recognize how nutrient-rich sites, especially those with high levels of nitrogen, are more vulnerable (Table 4.4). This relationship is supported by research findings that increased nutrient

levels, especially nitrogen, tend to favor invasive species (Byun et al., 2018; Ibáñez et al., 2021). Practitioner views on the effect of low nutrient availability on resistance seems to depend on the ecosystem in question. For example, one interviewee describes nutrient-poor soils as more resistant to potential invaders:

“A lot of these ***communities that are nutrient-poor can do well*** on their own to keep out invasions.”

Another practitioner references dune ecosystems as an association of low nutrient availability with increased vulnerability because the invasive species in that ecosystem are highly adapted to nutrient-poor soils.

Diversity

Practitioners associate high native diversity and plant cover with increased resistance for a variety of reasons that align with the role of plant diversity discussed in the literature (Chapter 2). Practitioners recognize several measures of diversity as increasing resistance including genetic, species, functional, and structural diversity (Table 4.4). Structural diversity is referenced

when practitioners talk about the roles of a strong understory and quality ground and canopy cover in a resistant ecosystem. One practitioner illustrates this point:

“...once the *natives are very well-established, the invasives have a really hard time* setting in and establishing themselves.”

This relates to a study by Byun et al. (2015) which finds that dense cover of native plants helps to increase resistance to invasion. Consideration of structural diversity is also reflected in practitioner discussions relating numerous open niches to increased vulnerability. If invasive species are well-adapted to conditions found at the invasion site, they may more easily occupy an existing or potentially empty niche in the invaded system. In addition, workshop attendees highlight the importance of keystone species, noting that their absence from a system can increase community vulnerability (Table 4.4).

Table 4.4 | Summary of community characteristics that practitioners associate with increased resistance or vulnerability to invasive plant species.

Increase Resistance	Increase Vulnerability
Natural disturbance regimes (normal intensity)	Anthropogenic disturbances, including management “scars”
Connectivity	Fragmentation
Low nutrient levels (in some systems) or other abiotic extremes	High nutrient levels or invasive legacies altering soil chemistry
Native diversity (species, functional, genetic, and structural)	Loss of keystone species or overabundant herbivores

II. In what ways do practitioners take a systems-based approach (vs. treating single species) to reduce invasive plants? What lessons have they learned?

Recognizing the Need for Systems-Based Approaches

There is widespread recognition among practitioners of systems-based approaches and even general systems thinking (Figure 4.3). When asked about resistance-based management more broadly, practitioners discuss abiotic and biotic drivers and temporal and spatial dynamics as ways to understand or assess how the system works. Workshop attendees also consider their ability to recognize when a system has crossed a point where it cannot be reversed: "...where invasive management won't turn the system back towards a native community." In general, practitioners know that systems thinking is important. This is evident in their view of invasive species management as only one facet of protecting "native community health," and it is likewise reflected in the perspective that overall habitat quality depends on much more than the management of one or two invasive species. Specifically, one interviewee notes that they manage for multiple species at once, while simultaneously considering

which management techniques might benefit the plant community overall. Other practitioners describe a similar mindset, trying to strike a balance between treating invasive species and protecting or promoting native species. For example, the quote below demonstrates an understanding that species removal efforts may not actually be improving the ecosystem as a whole:

"...I think that a persistent, undesirable consequence is that in a lot of sites, if it's starting at a high level of degradation, and **you're really trying to target one or two species**, you might be able to manage those species . . . **But you aren't necessarily improving the overall quality of the site**, and you're creating openings that nonnative species will be moving into."

Key Themes

Supporting Practitioner Quotes



Figure 4.3 | A selection of interview quotes that illustrate practitioner awareness of systems-based management and provide examples of the systems-based management techniques they already employ.

Although some practitioners discuss a need to shift management approaches, the shift they have in mind does not necessarily refer to a systems-based approach. One practitioner emphasizes this, saying:

“There needs to be a ***shift in the focus of the source of the plants***, controlling at the source, so ***where are these invasive plants coming from***, and focusing on that part of it.”

While this described shift is preventative, it is still single species-focused and does not affect the overall vulnerability or resistance of the system itself.

Systems-based management in practice

While several practitioners translate systems-based thinking into actual on-the-ground resistance-based approaches, these approaches are not a major component of their overall management strategy. Six of the eight interviewees talk about management practices like protecting the native seedbank, seeding natives, using native plantings to help shade out potential future invaders, and "proactively planting with early-successional natives to fill a

niche." In addition, one interviewee describes how they have reintroduced historic disturbance regimes to a site through fire. Other practitioners also utilize prescribed burns, but they do not necessarily frame this method as systems-based. Native planting actions are supported to some extent by research. Funk et al. (2008), for example, find that native plant selection is a crucial step in maximizing plant functional diversity and competitiveness. However, Byun et al. (2018) report that increased plant diversity alone does not result in a more resistant system. In any case, resistance-based approaches tend to be used sparingly in practice and in combination with invasive removal. Furthermore, the resistance-based approaches practitioners mention are often reserved for only certain management scenarios, such as complete site restoration after building removal, and not to proactively support existing plant communities.

Evaluating Success is Limited by Current Monitoring Efforts

Practitioners' ability to evaluate the success of resistance-based practices is restricted both by limited implementation of those approaches, as well as the measures used to evaluate success. In our interviews,

practitioners emphasize the difficult nature of evaluating management projects and their impacts. For example, they note that a lot of their success is anecdotal, and that evaluation often depends on qualitative judgement of whether a given approach was a “good use of someone’s time years ago.” Other lessons concern the relationship between practitioners’ goals and how they define and measure success. To illustrate, practitioners note that it is difficult to balance day-to-day work with longer-term goals: “...it can be hard to take a moment and really look at the big picture,” but they recognize that big picture consistency is essential. A common measure of success involves invasive presence and abundance:

“Success for us is largely if we **return to those sites year after year and we’re seeing decreasing abundances of invasive plants**, then that’s really success.”

Practitioners describe the qualitative land manager lens as the ability to know whether a site is generally in good or bad shape based on visual cues, such as looking for “little pockets of things that are good and historically found in these areas.”

Although practitioners have various monitoring efforts in place, they state that it can be difficult to interpret data to judge why management is or is not successful at a particular site or why treated areas have similar or different responses to management. Practitioners also note that it becomes difficult to evaluate overall site quality when most of the collected data they have access to is about invasive abundance. This lack of community-level monitoring data is one of several challenges practitioners identify to adopting resistance-based approaches.

III. What are the challenges to adopting resistance-based approaches? How do practitioner decision-making processes and structures (goal- and priority setting, funding, planning cycles, etc.) affect their ability to implement a systems-based approach?

Practitioners identify characteristics contributing to vulnerable versus resistant plant communities and understand the advantages of a systems-based approach to management. However, the practical considerations that influence decision-making can contribute to the disconnect between what practitioners would like to do and what they currently do. We found that practitioners identify six main decision-

making considerations relevant to invasive management practices: prevention, prioritization, efficiency/cost-effectiveness, collaboration, education/outreach efforts, and future directions. Prevention refers to practices that stop the spread and introduction of invasive species to sites, while prioritization involves selecting certain sites over others depending on variables such as site quality, site vulnerability, and site resistance. Cost-effectiveness considers how funding is allocated to invasive plant management projects. Collaboration refers to an organization's internal and external interactions. Education efforts involve the translation of information to the public and public involvement in projects. Finally, future directions relate to how practitioners envision invasive plant management unfolding in their respective organizations.

Each of these decision-making considerations relates to the main barriers practitioners identify to taking a more systems-based approach to invasive plant management. Below, we elaborate on the key issues that practitioners report as barriers to implementing resistance-based approaches in particular but also invasives management more generally:

1. *Information*: Lack of access to information or research to inform prevention, prioritization, and future directions.
2. *Collaboration and Organization*: Organizational challenges that hinder efficiency or cost-effectiveness.
3. *Funding*: Mismatch between funding and what is needed in the short- and long-term.
4. *Education*: Outreach needed to guide public perceptions and overcome social barriers.

Information

Practitioners identify research and information needs to inform decisions related to prevention, prioritization, and future directions that would also allow a shift to more resistance-based approaches. Currently, managers leverage their expert opinions, knowledge from professional colleagues, and guidance from existing policies/compliance to inform their decision-making with respect to invasives. In general, practitioners tend to focus their efforts on sites that are deemed “higher quality” or are in some way already “naturally more resistant.” Higher quality sites are prioritized because they are perceived as requiring less management, whereas lower quality sites may not recover as well from management disturbance and have the potential for secondary invasion issues. The following excerpts illustrate how practitioners rely on other professionals or existing laws and review structures for informing management decisions:

“Throughout the regional structure, there are **resource professionals** who are focused on invasive plant management that we can have questions with, and they **provide information and feedback** and reports out to the parks as well.”

“I will **consult ... the laws pertaining to the treatment that we are trying to do in the sites** to make sure that we're not damaging archaeological remains or... putting chemicals into a sensitive site or that type of stuff that will get reviewed by an interdisciplinary team, the IDT team, which has a representative from each division from maintenance, to law enforcement, to natural resources and interpretation. So the idea behind that is **we should all have an idea to see what the project is and think what it might impact** and we go through a checklist and a pretty formal process.”

Ultimately, practitioners’ decision-making comes back to identifying future considerations. Emphasis is on the need to manage for future resilience and maintain

consistency over time; the former is of particular concern in the face of uncertainties around climate change impacts.

Practitioners report that increased data accessibility and more experiences that build local and institutional knowledge would be most important in overcoming informational barriers to resistance-based approaches. They suggest creating an open-source data platform for the exchange of information. As they highlight, sharing data and knowledge is crucial to practice: “capturing information that people know but is not published...may be unused on the ground.” They point out a key need for “an alternative way of communicating science” that does not just rely on “phone and lunch conversations.” They also identify the need for more local studies to discern the drivers of and effective approaches to managing invasive species in the specific ecosystems they work in, rather than generalizing results from other systems. While practitioners identify a need for research on decision thresholds, they also recognize how challenging that might be:

“I think that what would be really nice as a manager and a practitioner would be to have **research-based ways of assessing the threat** and impact and setting treatment thresholds for something that was more true to an IPM [integrated pest management] approach, where different approaches might be triggered by different impacts on the environment. That’s of course pretty complicated because at that point, **you need to be thinking a little bit about what constitutes a functional, healthy ecosystem** and environment, which is a very debatable subject in and of itself.”

Demonstration sites are identified as a way to both capture local knowledge and provide real-time results of system-based restoration rather than species-level interventions. Practitioners need to know when an approach is or is not feasible and what alternative methods are available. Demonstration sites could provide that information. Other practitioners raise how meeting informational needs by improving record-keeping tools, modeling for long-term and larger-scale changes from invasion, and building understanding of hydrology pathways could aid in

management efforts. Thus, we recommend increasing opportunities for information exchange on invasive species and monitoring efforts,, as well as demonstration site-based research on the effectiveness of different resistance-based methods in local contexts.

Collaboration and Organizational Barriers

Organizational barriers, such as a lack of coordinated planning or communication, limit the implementation of resistance-based approaches. A comprehensive plan that builds in the capacity for management is essential. As one practitioner states, “Some sites had no cohesive site management plan and were very limited by being understaffed and underfunded.” At times, practitioners deal with different goals within the organization and challenges in integrating these goals across an ecosystem. Communication challenges within the organizations, such as interdepartmental misunderstandings, are reported to negatively impact the prioritization of sites and even education and outreach efforts.

The value of partnerships is evident in the context of maximizing efficiency and cost-effectiveness in management efforts -- especially with regard to balancing labor inputs with results. Managers and their staff

generally operate with a mandate to manage invasive plants across large geographical areas as part of a long list of other duties and so are constrained by competition from other responsibilities (Rentz et al., 2009). The potential for collaboration is emphasized in both the workshop and interviews, and practitioners highlight the opportunities to work across jurisdictions and use existing resources. As one practitioner states, “It’s not just about us and managing our land. There’s no boundary when it comes to invasive species. As land managers, we can work together as a region.” While practitioners stress that “connections need to be formed between small- and large-scale management,” a major barrier to implementing more systems-based or even larger-scale management is the institutional change required. As one practitioner states, “It takes time to shift what people are used to doing. There’s less capacity for doing a large-scale field restoration, less built-in experience.”

Partnerships appear to be a key way to not only increase organizational capacity but also to fill the information and expertise gaps that currently limit taking alternative approaches to invasive species management. We see a need for more partnerships, specifically partnerships with skilled tool users and researchers. This

would allow tools, like remote sensing and spatial imagery, to inform management (e.g. D'Antonio et al., 2004). Practitioners also struggle to incorporate Indigenous knowledge thoughtfully and respectfully. Formalizing partnerships could resolve this challenge. When practitioners expand their research and cross disciplinary boundaries, they gain new insights on how to manage invasive species from a systems-based lens (Matzek et al., 2014). One practitioner describes how partnerships can create opportunities to improve management practices particularly well:

“...one thing that I feel really lucky to have had in my career is **willing and expert collaborators** who ...just like...geek out to help out or **share their knowledge is really helpful**.

And oftentimes, we can get something off the ground much more rapidly when it's been tested somewhere else by **a partner that we value and trust**...so that can be really helpful.”

Similarly, within their organizations, practitioners stress the importance of taking advantage of existing partners and networks to educate their staff and interns regularly:

“[The] Invasive Species Network **provides training** and opens these up to the partners. It's good to go through the training on a regular basis. We like to make sure our interns and new staff members attend those training sessions.... [and have] **opportunities to talk to partners** from across the region and compare approaches.”

Funding

In practitioners' responses we frequently observe a mismatch between funding and what is needed in the short- and long-term. Grantors have influence over the acreage that is treated and the number of species that are being treated. This can influence the success of treatment, as well as long-term management efforts. Although huge investments are made in invasives management (e.g., \$4.9 million per year to manage one invasive species for five years; Martin & Blossey, 2013), others identify that invasive species managers frequently cite a lack of funding as barriers to their success

(Kuebbing & Simberloff 2015; Matzek et al., 2014; Renz et al., 2009 in Beaury 2020). We hear from practitioners that “funding is often not enough to fully treat an area,” so practitioners are partially treating. An even larger impediment that practitioners identify, especially to resistance-based management, is restrictions on how funding can be used and the time period of the funding. In particular, practitioners raise the issue of funds available specifically for removal but not for alternative treatments or for monitoring of short- and long-term success, as exhibited in the following quote:

“There is a ***lack of funding*** for long-term management and for learning.”

Overall, there is a clear need for funding and resources to monitor before and after management activities, to allow for follow-up treatments, and even for outreach and education efforts related to invasive species management.

Education and Outreach

Practitioners identify an increased need to communicate and educate the public on current invasive management projects, treatments employed, and opportunities for public involvement. When practitioners focus on engagement, they try to interact with groups of people, using an extensive local network, to disseminate information. Practitioners also suggest that “there could be some K-12 system outreach to achieve youth and then adults through them.” Research on engagement also finds that more reporting by the media and increased K-12 education about invasive plants provides broader support for invasive plant research and management (Renz et al., 2009).

Differences in landscape perception and cultural values can also shape how action proceeds. Practitioners note that a significant barrier to public involvement is an attachment to the aesthetic quality of some invasive species, especially on private land. Moving public perception from a purely aesthetic focus to an ecological focus is quite a hurdle for practitioners because it requires communicating the potential harm of non-native species, and landowners may be resistant to this information. Some practitioners also face social pressure from community members who donate to natural

area preservation and have strong opinions that run counter to management practices. Misunderstandings result in large amounts of time and money being spent to defend management actions (e.g., public surveys, litigation). For example, one practitioner describes a case where managers were sued for cutting trees down in a mesic woodland restoration to prairie. Practitioners who work with different landowners that own property with invasive species also stress the challenge in dealing with unwanted consequences of invasive species removal (e.g., browning due to herbicide treatment). This suggests that in some instances, resistance-based approaches (e.g., native plantings) may be more aesthetically acceptable to the public, even with less outreach effort, than some removal efforts.

We hear from practitioners that public perception of invasive species present in their nearby landscapes can differ greatly from what a practitioner in the field experiences and researches. Practitioners raise the idea that taking volunteers to high-quality areas that may be more difficult to reach rather than low-quality, easy-access areas can help build public understanding of the value of an intact ecosystem instead of only focusing on the invasive species present in the area. When volunteers are at

these high-quality sites, noting the ecosystem services provided by the plant community can help reframe their perception of the site. In this sense, on-the-ground examples of goal ecosystems may be important for motivating and setting up realistic ideas about potential outcomes of management. By identifying differences in values and landscape perceptions, practitioners can target outreach and education to support a shift toward systems-based management, while still maintaining public awareness of particular invasive species.

Conclusion

I. What characteristics do practitioners associate with more vulnerable or more resistant plant communities?

Overall, we find that practitioners discuss vulnerability concepts more often than resistance characteristics. In addition, when asked to describe what characteristics of an ecosystem make it more vulnerable or resistant, practitioners repeatedly reference traits of invasive species themselves, such as dispersion, phenology, and competitive ability. This reflects the dominant focus on species-specific traits that commonly guides current invasive management practice. Further questions to better understand on-

the-ground perspectives and practice include:

- Is the focus on vulnerability traits because characteristics of resistance are less understood, or because fewer factors cause resistance than vulnerability?
- Does the focus on vulnerability traits translate into a stronger focus on management to prevent or reduce vulnerability, rather than actively promoting resistance?

Practitioners generally agree on which characteristics relate to community vulnerability and resistance (Table 4.2). Their perspectives, though largely in line with current research, are more complex and nuanced than is discussed in the literature. These findings have important management implications and highlight the need for more region-specific research on these topics with extensive follow-up to monitor results and record practitioner perspectives. We recommend the following questions for future research on this topic:

- To what extent do the causes of vulnerability and resistance depend on the local ecosystem's characteristics and history?

- Do practitioners focus on vulnerability traits because characteristics of resistance are less understood, or because fewer factors cause resistance than vulnerability?
- Does the focus on vulnerability traits translate into a stronger focus on management to prevent or reduce vulnerability, rather than actively promoting resistance?

II. In what ways do practitioners take a systems-based approach (vs. treating single species) to reduce invasive presence or impact? What are the lessons they have learned?

Throughout the workshop and interviews, practitioners frequently discuss the need for more holistic, systems-based strategies. Although practitioners provide numerous examples of how they are thinking about or considering systems-based practices and relationships at a site, there is a disconnect between systems thinking intentions and on-the-ground implementation. Of the systems-based practices that are implemented, practitioners mostly focus on the addition of native seeds or plants to support biotic resistance or in some cases use prescribed burns as a way to restore disturbance

regimes; however, they do not tend to manage abiotic conditions which is a potentially useful approach for increasing resistance (Chapter 2). This raises several interesting questions for future research:

- Are these resistance-building alternatives not used because they are not well understood or not as easy as plant-addition practices or prescribed burns?
- How could these strategies be used as stepping stones to build upon and incorporate other systems-based strategies?
- Why are planting additions used in complete restoration sites instead of applied to existing communities to fill functional gaps and prevent invasion?

Common monitoring efforts utilize the presence and abundance of invasive species as ways to assess management success, which do not align well with systems-based management approaches that would assess native community diversity. Although the role of institutional knowledge (e.g., manager's expert and long-term qualitative site assessment) guides site prioritization and management action, the focus on invasive species can be limiting because it

does not necessarily provide information about the status of the native plant community. This disconnect can make it difficult for practitioners to interpret monitoring data and evaluate overall site quality. The questions below aim to better understand this dynamic:

- How is institutional knowledge saved and transmitted, if at all?
- How can this information be incorporated into recommendations for more effective, systems-based monitoring efforts?

III. What are the challenges or barriers to adopting resistance-based approaches? How do practitioner decision-making processes and structures (goal- and priority setting, funding and planning cycles, etc.) affect their ability to implement a systems-based approach?

Practitioners cited four main barriers to the implementation of systems-based management approaches: access to information, organization and collaboration, funding, and education and outreach. In order to address these barriers we recommend the following approaches:

1. Increase practitioner access to, and exchange of, information and research that would allow for

changes in current management practices. Establish demonstration sites of resistance-based approaches to share and communicate methods and outcomes.

2. Encourage collaboration and partnerships among practitioners for sharing knowledge and data that can lead to new insights and tool use to increase capacity for systems- and larger-scale approaches.
3. Increase funding not just for removal but for implementing alternative methods, and for learning. Funding must cover efforts to monitor native community diversity (and other success measures besides invasive species abundance) before and after management practices and support related education and outreach efforts.
4. Further investigate how outreach resources can be used more effectively to increase public understanding and interest especially in systems-based invasive species management (For an Education and Outreach interview guide that could inform this research see Appendix D).

In conclusion, practitioner work already exemplifies many conclusions drawn in current research with the distinct difference that practitioner perspectives add nuance and functionality to knowledge on invasive species management. The results of this chapter underscore the importance of closing the gap in the field of invasive species management between research (“knowing”) and practice (“doing”). Our results show that practitioners hold knowledge that is not discussed in invasive species research. Not only do practitioners discuss the need for and benefits of increased engagement with research, but research can benefit from engaging with the experiences of practitioners, especially those that are not in line with current research conclusions. Hearing the expertise and experience of practitioners who keep a continual pulse on shifting ecosystems can lead to new research discoveries while also providing useful information to inform more efficient and effective invasive species management practices.

Appendix A: Research Brief



Research Brief

Content organized by: Sara Steenbergh, Gabrielle Vinyard, and Sheila Schueller

Managing for Ecological Resilience

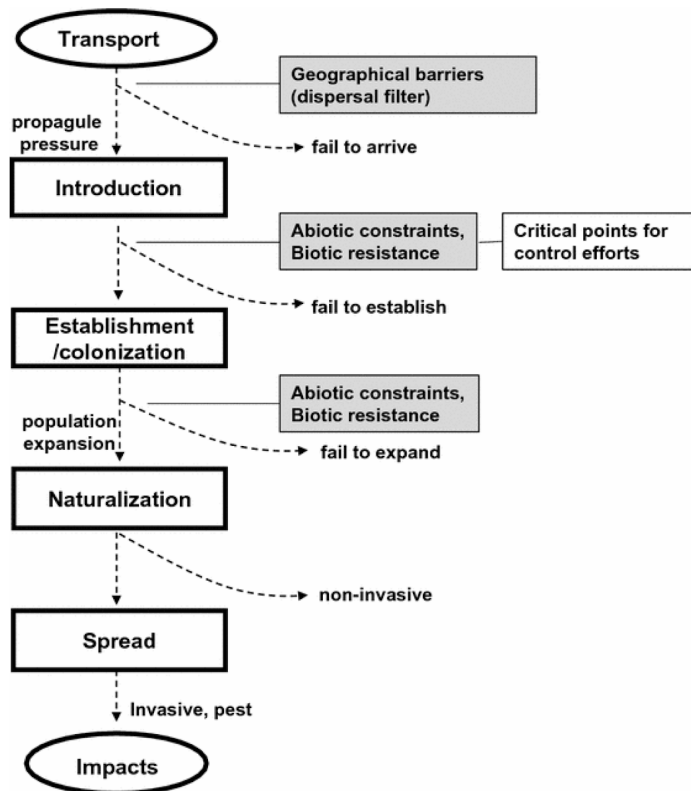


Figure from Byun C, de Blois S, Brisson J (2018) Management of invasive plants through ecological resistance. *Biol Invasions* 20:13–27.

Whether managing for *resilience* (long-term return to a desired community state) or *resistance* (reduced change or impact of invasives on a community), there are several possible points of intervention.

Successful invasive species establishment or impact could be achieved by reducing propagule pressure and/or by increasing or maintaining abiotic (physical) or biotic (biological) filters of the community.

The following page provides a sample of possible management options related to presumed mechanisms of resistance.

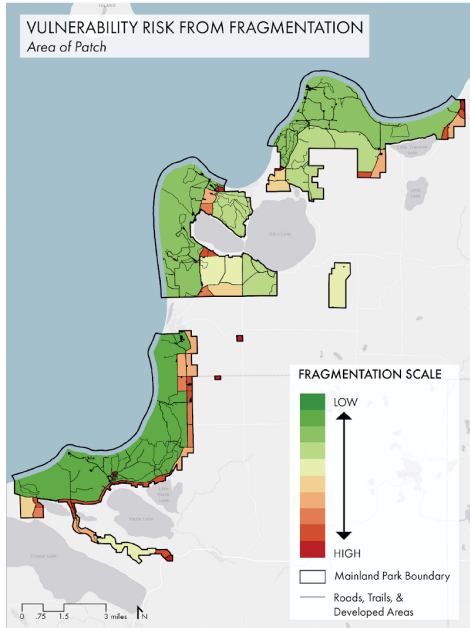
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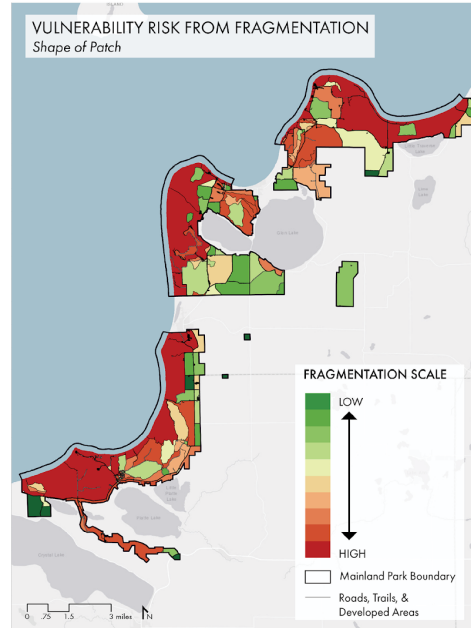
	<u>Theory</u>	<u>Potential Management Options</u>
INPUT	Propagule pressure: How much and how often non-native seeds or propagules are entering the community.	➔ Reduce sources of non-native seeds in seedbank or surrounding areas or overwhelm with native seed: E.g. Sowing <i>Gaillardia pulchella</i> at high density (10g/m ²) reduced 83% of <i>Rapistrum rugosum</i> invasion by seeds ¹ .
	Environmental stress: Extreme environments suppress intolerant species	➔ Create environments the invasive does not tolerate as well as the native species: E.g. Flooding inhibited <i>Phragmites australis</i> while at least some native species tolerated it ⁵ .
ABIOTIC	Resource Availability: Environments with more nutrients, water, light, or space (bare ground) are less resistant.	➔ Alter resource availability : E.g. In areas invaded by <i>Phalaris arundinacea</i> , applying saw dust lowered available nitrogen in soil, delaying establishment and reducing invasion by 59% ⁶ .
	Diversity: Communities with higher species richness are more resistant to invasion because all the niches are occupied	➔ Revegetate with seed mixes: E.g. mixtures of four native wetland species were more resistant than single species plots to invasion by <i>Phragmites australis</i> ² .
BIOTIC	Functional Diversity: A species cannot occupy a niche that is already taken by a species that is similar to it (related to the idea of "limiting similarity")	➔ Increase natives with similar function to the invader: E.g.: Even monocultures are resistant to invasion by <i>Bromus tectorum</i> (an annual grass) or <i>Isatic tintoria</i> (a biennial forb) <u>if</u> they are the same growth form as the invader ³ .
	Priority effect: Who gets there first wins ("first come, first served")	➔ Revegetate with fast growing, early emerging plants: e.g. Of 35 native wetland plants, fast-growing annual species were most resistant to the invasive grass <i>Phalaris arundinacea</i> ² .
	Competition: Species with allelopathy, high biomass, or ability to outcompete for resources can prevent invasives	➔ Increase or maintain native competitors: e.g. <i>Ailanthus altissima</i> population growth was most effectively suppressed when the absence of fire increased native competitors. ⁴
	Enemy release hypothesis: Invasive species are largely free of native predators	➔ Biocontrol measures or controlled grazing. Specialized non-native leaf-feeding beetles have been effective biocontrol agents of purple loosestrife (<i>Lythrum salicaria</i>)

Appendix B: Map of land parcels within park boundaries fragmented by development, showing AREA and SHAPE metrics separately. Shown on a scale from least to most fragmented in green to red.

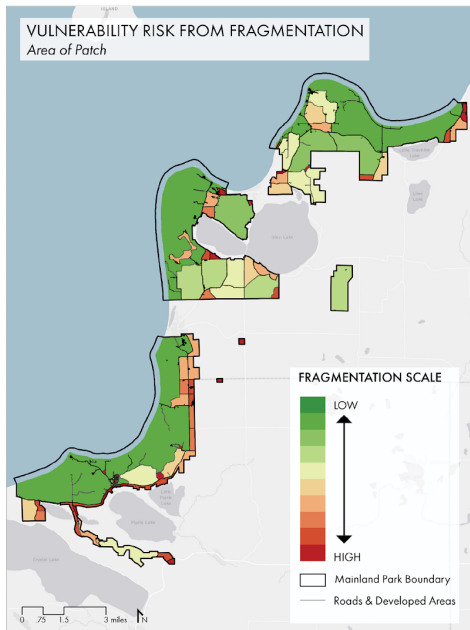
ALL DEVELOPED AREAS



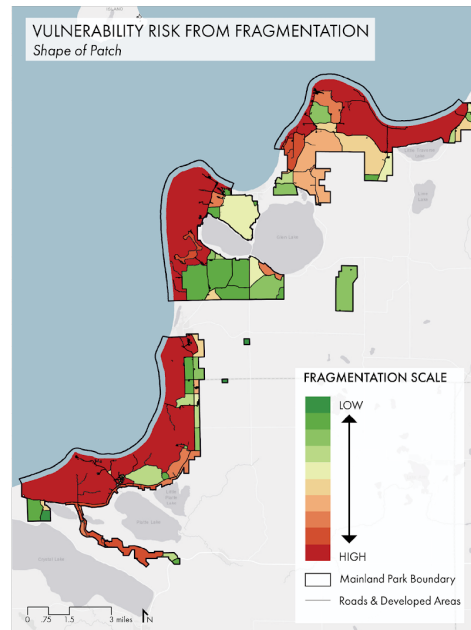
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DEVELOPED AREAS, EXCLUDING TRAILS



+



Appendix C: Practitioner Interview Guide (Management)

Introduction

Good morning/afternoon [insert name of professional]. I hope you are doing well during these stressful times. [Introduce yourself here first]. I'm a second year MS student at SEAS in... background in..., and I'm working with a team of 5 other students on a capstone project where we work with a client to address a sustainability problem. We are interested in how to make plant communities less vulnerable and more resistant to invasion by non-native plants. Specifically, we are working with Sleeping Bear Dunes National Lakeshore on their restoration and invasive species control needs. In particular, Sleeping Bear Dunes National Lakeshore staff have asked us to assess alternatives to a single species-focused management approach to invasives. I was also present at the "Reframing Invasions" Workshop back in February as a student facilitator and found the conversations to be very insightful. Our project is being supervised by Dr. Sheila Schueller, who co-led the workshop with Dr. Inés Ibáñez.

I really appreciate you taking the time to meet with me, because the purpose of this interview is to really understand the needs and realities of invasive species management from *your* perspective. That is, as someone who has on-the-ground experience and expertise in invasive management. Specifically, I hope to get your input on three main questions:

- 1) What are characteristics of resistant or vulnerable plant communities?
- 2) How can or do you manage your sites to increase resistance or reduce vulnerability?
- 3) What do you see as the barriers to these approaches?

Ultimately our team wants to apply what we learn from you to inform recommendations for Sleeping Bear Dunes National Lakeshore, but we also see this as an opportunity to create lessons and recommendations that can apply to any site. This interview will take approximately one hour, and I am happy to send you a copy of the interview transcript afterwards. This interview will be distributed among the team members and with our advisor, Sheila Schueller. We will be incorporating this interview into our final report. Would it be okay with you if I record this interview? It would help me in capturing your input accurately. You are welcome to stop me at any point if you need me to clarify anything. Do you have any questions before we begin?

A. I'd like to start with just some background about what you do so we can understand how experiences and sites differ among the people we interview.

1. *What are the key ecosystem types that you manage?*

2. *What is the scale of your management units? How large is the whole area?*
3. *Which of the ecosystems or sites that you manage are most vulnerable to invasives (that is, have the highest rates of invasion)?*
 - a. *What disturbances are you seeing? What do you consider to be a disturbance?*
 - i. *Natural disturbances?*
 - ii. *Anthropogenic disturbances?*
 - iii. *What do you do after a disturbance?*
 - iv. *Do you consider invasive management a disturbance/certain practices in invasive management?*
 - b. *Do you think vulnerability varies by ecosystem or type?*
4. *Why do you think so? What about those communities do you think makes them more/less vulnerable?*
 - a. [prompts if no answers - *Do you have different disturbances, diversity, ...list some of the key variables*]
5. *How do you define native species?*
 - a. *Do you consider future habitat conditions in your definition?*
6. *On the flip side (if it didn't already come up), are there ecosystems or sites that you manage that are more resistant to invasion?*

B. Now I'd like to get into understanding your management approaches and how you prioritize certain management techniques over others.

7. *What are the most common tools/approaches you use to control invasive species presence or impact in these ecosystems?*
 - a. (If they differ by species - What are the approaches for the three most common invasives?)
8. *What are the alternatives to herbicide? Have you used biotic resistance methods such as seeding of natives (insert examples here)? What do you know about biotic resistance?*

The following questions focus on resistance-based approaches and whether practitioners are using them and which ones they are using specifically. What do we know about resistance-based approaches? Are practitioners using them? Which ones? If a practitioner asks for an example on what resistance-based approach, there are three factors that determine the outcome of an invasion: biotic resistance, abiotic constraints, and propagule pressure. Biotic resistance refers to the ability of species to resist or limit invasion. This can be from niche and fitness differences,

diversity effects, and competition. It is the ability of a plant community to reduce the success of exotic plant invasions. Abiotic constraints refer to the environmental conditions that can limit the success of an invasion such as limited nutrients, low light levels, etc. Propagule pressure is the number of individuals arriving at any one time, and management practices can include the elimination of an on-site seed bank. (Byun, Blois, and Brisson 2017).

9. *In what ways have you taken a systems-based approach (vs. treating single species) to reduce invasive presence or impact? For eg. by managing the characteristics of the community that makes it vulnerable or resistant [x from their list]? Have you ever tried...[some from Byun] lowering nitrogen availability with sawdust? What other techniques have you implemented?*

- a. *If so, what has worked? Not worked?*
- b. *What happened when it didn't work? [unintended consequences]*
- c. *How do you think the effectiveness compares with species-based approaches?*
- d. *What is "success?" How do you know it worked?*
- e. *How are you monitoring the success?*

C. We are going to transition into the next questions that will focus on barriers to taking a systems-based approach and the future of invasive species management.

10. *What do you think are the biggest challenges or barriers to taking a systems-based approach to invasive species management? [open-ended first and then prompt each of the below]*

- a. *Capacity? [funding, labor, time]*
- b. *Institutional barriers?*
- c. *Public perceptions?*

D. The next set of questions help us understand how practitioners make decisions, their decision-making process, and the information they rely on in making decisions.

11. *What are the barriers to applying new ways of managing invasives?*
12. *What would facilitate applying alternative approaches?*
13. *Do you use adaptive management?*
14. *Given the processes for decision-making, how can we best integrate our recommendations/new approaches?*
15. *How do you make decisions?*
 - a. *Where do you get info that informs your decisions?*
 - b. *X over Y?*
16. *What are your short and long-term goals?*

17. I want to end with a big question, feel free to answer with any general thoughts or ideas you have on this topic: Given continued invasions, climate change, and other stressors, what do you see as needed for the future of invasive species management?

Appendix D: Practitioner Interview Guide (Education & Outreach)

Introduction

I'm a second year MS student at SEAS in... background in... I'm working with a team of 5 other students on a capstone project where we work with a client to address a sustainability problem. We are working with Sleeping Bear Dunes National Lakeshore on their restoration and invasive species control needs. In particular, Sleeping Bear Dunes staff have asked us to assess alternatives to a single species-focused management approach to invasives, so we are interested in how to make plant communities less vulnerable and more resistant to invasion by non-native plants. Our first round of interviews focused on learning from invasive species management practitioners. Specifically, our goals were to understand more about the characteristics of resistant or vulnerable plant communities, how practitioners manage their sites to increase resistance or reduce vulnerability, and what they view as the barriers to these approaches.

Our goal with these interviews is to help understand what kind of invasives outreach and education is most effective and how challenges in public involvement or understanding of the issues can be overcome. *Specifically, we're interested in helping improve public understanding of systems-based approaches to invasive plant management, such as increasing overall ecosystem resistance to invasives and reducing vulnerability, vs. a single-species strategy to address the problem.* We'd like to share this information with Sleeping Bear and other organizations that are working with the public on invasive species management, and I hope to get your input on your current approaches to increase public awareness on invasive plant species and your successes and challenges in *educating* the public on invasive issues.

First, I'll ask some background questions to get a better idea of your role and your organization's structure. Then we'll get into your current outreach and education goals and the methods you employ to achieve these goals. Afterwards I'll follow up with questions about the successes and challenges that you face. Finally, I'll finish by asking how you have adapted your outreach and education program over time and how you see it changing as you move forward. Do you have any questions on the purpose or structure of this interview before we start? Is it okay if we record this interview so that it can be easily transcribed later?

A. Organizational Background

1. *What is your role in the organization?*

2. *How does your role/O&E efforts fit into the broader activities of the organization, especially with regard to invasives management?* [organization's structure- Is it a whole arm, one person with multiple jobs, collaboration with other organizations/agencies etc.]

- a. *How do you coordinate [if applicable] between departments within your organization?* [cross-educate staff members?]

B. Goals and Current Approaches

3. *What are your current O&E goals in terms of invasive species management?*

- a. *Are these goals centered around more systems- or species-based approaches?* [how do they *frame* invasives management?]
- b. *How do you define effective education?*

4. *What O&E methods are you currently using to help achieve these goals?* [in-person & virtual presence, visuals, volunteering, how information is distributed to the public, etc.]

- a. *How effective are these methods?* [are they helping you meet your goals?]
- b. *How do you choose what information to provide/focus on?*
- c. *Can you provide an example or two of successful education efforts and outcomes?*

5. *How do you coordinate O&E efforts within your organization/preserve boundaries with your O&E efforts within the surrounding community?*

- a. *Are these O&E efforts different?*
- b. *How could coordination efforts be improved?* [if applicable]

6. *Do you discuss/present invasive treatments/management?*

- a. *If so, how?*
- b. *What issues or concepts are the most difficult to convey to a public audience?*

7. *How do you define key terms like invasive, resistance, vulnerability, disturbance, and adaptive management?* [if they utilize these terms]

- a. *Are there other important terms/concepts that you often use?*

8. *What audience(s) are you trying to reach?*

- a. *How successful have you been in reaching and engaging those audiences?*

9. *How do you keep your education efforts accessible and inclusive? [in terms of different ages, abilities, languages, etc.]*

a. *How could this be improved?*

C. Logistics and Future Directions

10. *Where do you get your funding for O&E? [if they have funding specifically designated for O&E purposes]*

a. *How does this support or complicate your O&E work?*

11. *What is your process for developing and adapting your O&E program over time?*

a. *How do you track/monitor success? [if this hasn't already been covered]*

b. *How do you receive feedback on your programming from visitors/the general public?*

i. *What type of feedback have you noticed? [generally positive, negative, etc.]*

ii. *What do you do with the feedback?*

12. *Are your O&E goals and/or approaches different now than they were in the past? [if this hasn't already been covered]*

a. *If so, how?*

b. *Have you seen a shift from a species- to a systems-based approach?*

13. *What direction do you think O&E efforts need to go in the future?*

14. *What would help you incorporate or work towards that future direction?*

15. *Are there any other challenges towards achieving effective O&E that you would like to add/elaborate on?*

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