

Determinants of biotic resistance to invasion
in plant community reassembly

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"I will now try and set out some of the evidence that the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that [the balance] is more subject to destructive oscillations in populations, especially of animals, and more vulnerable to invasions ... "

Charles Elton (1900 –1991)

The Ecology of Invasions by Animals and Plants (1958)

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ABSTRACT

Biotic resistance refers to the ability of species in a resident community to restrict invasion. Biotic resistance is central to our understanding of how a community recruits/repels new species. From a practical perspective, biotic resistance is relevant to the restoration of communities and/or the management of invasive species. In spite of advances in community ecology, fundamental ecological mechanisms regulating biotic resistance are not fully understood.

This research investigates determinants of biotic resistance to invasion. Its overall objectives were to identify the characteristics of species and communities making them more or less resistant to species invasion and to quantify the contribution of other biotic and abiotic factors to the regulation of biotic resistance. I hypothesized that (1) functional group identity of wetland species would be a good predictor of their biotic resistance, while species identity effect would be redundant within functional group; (2) mixtures of species would be more invasion resistant than monocultures; (3) abiotic constraints (flooding in this case) would influence biotic resistance both through direct effect on invaders and indirect effect on resident wetland species, and (4) propagule pressure of

invading species would interact with wetland plant density to influence biotic resistance.

I chose an introduced lineage of *Phragmites australis* as a model invasive species to test biotic resistance, but used emergent functional groups of wetland species based on trait similarity to facilitate generalizations to other species. I conducted a series of rigorous community assembly experiments both in pots and in wetland to simulate a situation where *P. australis* seeds land on bare soil along with other wetland species, a common occurrence in the field after disturbances or wetland restoration. Biotic resistance was estimated by comparing *P. australis* emergence in experimental treatments (i.e., both *P. australis* and wetland plants were applied) to control group (i.e., only *P. australis* seeds were applied). I used advanced statistical approaches based on diversity-interaction models to disentangle species interaction mechanisms underlying diversity effect and structural equation models to estimate effect of flooding on invasion.

Strong resistance of short fast-growing annual plants to restrict *P. australis* emergence was one of the most consistent findings across several experiments. This result suggests priority effect as a mechanism regulating biotic resistance to

prevent seed-mediated invasion of *P. australis*. Regarding the diversity-invasibility relationship in community assembly, combining certain functional groups in specific ratio led to complementarity diversity effect which strengthened biotic resistance. This result implies species interactions between functional groups are key mechanisms generating diversity effect. Structural equation model supported a partial mediation hypothesis in which both direct flooding effect on *P. australis* and indirect flooding effect on wetland plants determined invasion success. Abiotic constraint and biotic resistance worked synergistically or antagonistically in controlling invasion depending on the fitness of the wetlands species involved. Finally, propagule pressure increased invasion success up to a threshold beyond which additional *P. australis* seeds did not increase invasion proportionally. This threshold was controlled by the species recruitment rate (i.e., seed density) of wetland plants, decreasing with increased density of wetland plants.

By embracing complex invasion processes and multiple drivers, my research not only advances our comprehension of early community assembly and response to invasion, but also proposes a useful analytical framework that I hope will inspire future investigations and experimentations in community ecology. The fields of restoration ecology and invasion ecology, in particular, are in dire need of strong

quantitative evidence to support ecological management approaches. This study can be an important step toward predicting invasion risk and impact as well as designing native community assembly for invasive plant management.

RÉSUMÉ

La résistance biotique fait référence à la capacité des espèces d'une communauté résidente à résister aux plantes envahissantes. Elle est un concept central à la compréhension des mécanismes responsables du recrutement ou de l'exclusion de nouvelles espèces dans une communauté. Les principes de résistance biotique peuvent être mis en application dans la restauration des communautés ou le contrôle des espèces invasives. Malgré les progrès récents en écologie des communautés, les mécanismes écologiques fondamentaux qui régissent la résistance biotique demeurent peu connus.

Les objectifs principaux de ma recherche étaient d'identifier les caractéristiques des espèces et des communautés les rendant résistantes à l'invasion, et de quantifier la contribution d'autres facteurs biotiques ou abiotiques susceptibles d'influer sur la résistance biotique. J'ai émis l'hypothèse que (1) le groupe fonctionnel des espèces est un bon indicateur de leur résistance biotique ; (2) les combinaisons d'espèces sont plus résistantes à l'invasion que les monocultures ; (3) les contraintes abiotiques ont un impact sur la résistance biotique par un effet direct sur les plantes invasives et par un effet indirect sur les espèces résidentes, et (4) la pression de propagules des espèces envahissantes interagit avec la densité des espèces résidentes pour contrôler la résistance biotique.

J'ai choisi *Phragmites australis* comme plante envahissante modèle. J'ai réalisé une série d'expériences de recombinaison des communautés, en pots et en milieu humide, simulant une situation où des semences de *P. australis* arrivent sur sol nu simultanément à celles d'autres espèces, une réalité fréquente après perturbation en milieux humides. La résistance biotique a été évaluée en comparant l'émergence de semis de *P. australis* dans les traitements expérimentaux (*P. australis* avec d'autres espèces) au groupe témoin (*P. australis* seul). J'ai utilisé des modèles d'interaction-diversité pour distinguer les mécanismes d'interaction entre espèces qui sous-tendent les effets de diversité, et des modèles d'équation structurelle pour estimer l'effet de l'immersion sur l'invasion.

La forte résistance des espèces annuelles pour limiter l'émergence de *P. australis* suggère que l'effet de priorité est un des mécanismes qui détermine la résistance biotique à l'invasion. Concernant la relation diversité-invasibilité, un assemblage de groupes fonctionnels selon un ratio précis mène à un effet de complémentarité-diversité qui accentue la résistance biotique. Ce résultat implique que l'interaction entre espèces de différents groupes fonctionnels est un mécanisme clé générant l'effet de diversité. Le modèle d'équation structurelle

supporte l'hypothèse selon laquelle l'effet direct de l'immersion sur *P. australis* et l'effet indirect sur les plantes résidentes se combinent pour déterminer le succès d'invasion. Les contraintes abiotiques et la résistance biotique interagissent de façon antagoniste ou en synergie pour déterminer l'invasion. La pression des propagules augmente le succès d'invasion, mais il y a un seuil au-delà duquel davantage de semences de *P. australis* n'ont que peu d'effet sur l'invasion. Ce seuil semble d'autant plus bas que le taux de recrutement des espèces résidentes est élevé.

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PREFACE & CONTRIBUTION OF AUTHORS

This thesis is based on three manuscripts. Chapter 3 was published in *Journal of Ecology* and Chapter 4 was published in *Oecologia*. Chapter 5 will be submitted to scientific journal. Authorships are shown in the front page of each chapter.

Contribution of authors

All elements of this thesis are considered as my original scholarship. In each study, I defined research goals, proposed research hypotheses, and designed all experiments under guidance of thesis supervisors. I conducted all experiments with help of assistants, performed the statistical analyses, data interpretation, and discussion. I wrote the first draft of all thesis chapters, including the three manuscripts as a primary author. I also presented the main results of Chapter 3-5 at several international conferences, including Ecological Society of America.

My supervisors, Prof. Sylvie de Blois (McGill University) and Prof. Jacques Brisson (University of Montreal) proposed the overall research theme about biotic resistance to *P. australis* and funded the research. They provided guidance and resources for setting up the experiments and revisions based on manuscripts that I first wrote. They assisted in the publication process of my articles (Chapter

3 and 4). Both of them agreed for me to include two published manuscripts (Chapter 3-4) and one manuscript to be submitted (Chapter 5) in my thesis.

Original scholarship and contributions to knowledge

This thesis presents cutting-edge findings from three original studies, based on mesocosms and field experiments as well as modeling, on inhibitors of *P.*

australis invasion. It contributes to elucidate fundamental mechanisms of biotic resistance of relevance to invasive plant management. It provides new guiding principles for predicting community invasibility based on advances in ecological theory. It has the potential to influence the development of new invasion hypotheses related to the role of functional groups as biotic resistance is determined by functional group composition in plant communities and it is affected by abiotic constraints and propagule pressure. The interest for these findings is in part confirmed by the publication of an article in a high-impact journal, *Journal of Ecology* (IF: 5.431; ISI Journal Citation Reports® Ranking 2012: 14/136 (Ecology); 11/195 (Plant Sciences)).

My research contributes to advancing invasion theory by identifying primary invasion processes based on ecological niches. In chapter 3, I showed functional group identity in a plant community is a good predictor of its resistance to *P.*

australis invasion, while biotic resistance is redundant within each functional group. Moreover, most studies to date have used pre-defined functional groups (e.g., annual or perennial; forb or herb) to characterize species in related studies, but, to my knowledge, I am the first to use functional trait information to categorize species into emergent functional groups based on trait dissimilarity in relation to resistance to invasion. The results show that these trait-based emergent functional groups can be good predictors of biotic resistance.

My second study provides rare quantitative evidence based on rigorous experimental tests that there are significant interactions between biotic resistance and abiotic constraints as well as propagule pressure. Disentangling complex invasion processes is only possible through a synthetic and comprehensive approach addressing multiple interacting factors in community and invasion ecology. Most studies so far addressed one specific factor but did not focus on the interaction aspect. For these reasons, in Chapter 4, I designed a factorial experiment and applied a structural equation model to quantify the cause-effect relationships among major invasion factors. Once we understand how these factors interactively influence invasion, it may be possible to enhance synergetic effects among factors by selecting species best adapted to a given set of abiotic conditions to maximize biotic resistance to invasion. This knowledge may also

help predict the outcome of community assembly and invasion based on knowledge of the ecology and functional traits of the species involved.

My third study in chapter 5 shows, for the first time, that interactions between certain pairs of functional groups mainly drive the diversity effect underlying biotic resistance while certain functional groups selectively restrain a specific invader.

Using a model selection approach enabled me to quantify the relative importance of each mechanism by comparing candidate models. The multimodel inference has many benefits over direct comparison between two models, given that the models do not need to be constructed in nested equations. In particular, I analysed experimental data with the mixed-effect “diversity-interaction model”, recently developed but not tested for biotic resistance to invasion prior to my study. Using this approach makes it possible to evaluate and synthesize multiple mechanisms in a single study by means of a field experiment (Chapter 5).

Reducing complexity facilitates identification of the primary drivers that govern the diversity-invasibility relationship, and the simultaneous discrimination of the relative roles of functional group identity and the covariant of flooding.

By embracing complex invasion processes and multiple drivers, my PhD research not only advances our comprehension of early community assembly

and response to invasion, but also proposes a useful analytical framework that we hope will inspire future investigations and experimentations in the fields of community, invasion, and functional ecology. Besides the potential of my study to make a significant contribution to these fields, it has extensive implications for invasive plant management and ecological restoration. It will assist local managers in protecting ecosystems from potential invaders, especially but not exclusively *P. australis*, by proposing efficient restoration practices based on ecological principles and using invasion-resistant seed mixtures for restoration of invaded sites. The field of restoration ecology and invasion ecology is in dire need of strong quantitative evidence to support ecological management approaches. This is the first comprehensive study that provides an extensive field- and microcosms-based experimental assessment of the relevance of biotic resistance to the control of one of the major plant invaders in wetlands of North America currently largely managed through the use of herbicides.

Chapter 1 Introduction

1.1. Research background

Biological invasion is a major threat to ecosystem integrity and functions (Simberloff 2005). Once invasive plants spread outside of their native range, they can establish rapidly and form dense stands, replacing native species. They may also affect habitat quality and ecosystem services by altering habitat structure and interfering with original biogeochemical processes. Wetlands are particularly vulnerable to invasion. Although wetlands constitute 6% of the world's land mass, 24% of all invasive plants are found in this habitat (Zedler and Kercher 2004). *Phragmites australis* (common reed) is one of the most invasive wetland plants (Marks et al. 1994, Ludwig et al. 2003). Its exotic genotype (haplotype M) cryptically invaded North America over a century ago (Saltonstall 2002) and has since spread aggressively, curtailing native diversity (Warren et al. 2001). Its characteristic high tolerance to disturbance and phenotypic plasticity make it one of the most widely distributed invaders in natural history. Global warming may further favor its spread by altering phenology (e.g. extending its period of seed dispersal) (Wolkovich and Cleland 2010).

Current status of knowledge

In order to develop strategies to control and manage invasive plants, one must first understand the causes of invasion and its mechanical processes. Searching for the main drivers of invasion has been a central issue in invasion ecology (Mack 1996, Mack et al. 2000). Ever since Charles Elton proposed that more diverse communities would be less susceptible to invasion or more resilient to changes (Elton 1958), there has been a search for overarching principles governing invasion processes coupled with local community assembly (Levine and D'Antonio 1999, Callaway and Maron 2006, Fridley et al. 2007). In spite of the long history and important developments in invasion ecology, our understanding of how species interact in a variable environment, or which factors make communities more or less resistant to invasion, remains surprisingly limited.

Contradictory patterns in diversity-invasibility relationships across scales, the invasion paradox, reflect the multifaceted nature of the invasion process, in which propagule pressure, abiotic, and biotic factors are interactively involved (Fridley et al. 2007). It is unlikely that a single mechanism (or factor) governs the entire invasion process (Sax et al. 2007, Catford et al. 2009). We have arrived at the crossroad: it is time to attempt to understand the invasion process by putting together all the pieces of the puzzle and simultaneously addressing multiple drivers of invasion dynamics to see the big picture.

We also need to prepare for future challenges to wetland ecosystems by developing effective management strategies to control/prevent the spread of invasive plants, while restoring original, native communities. Still, there is a big gap between knowing and doing in invasion ecology (Esler et al. 2010). For instance, suggestions about how to manage or restore invaded ecosystems are generally neglected in major scientific journals. Invasive plants are commonly controlled by conventional eradication methods such as mowing or spraying herbicides, which have only a temporary effect. Most conventional control measures are ineffective against *P. australis* because of its high tolerance to physical stresses and great plasticity in the face of fluctuating abiotic factors. Only repeated, long term application of herbicide (e.g. several years) may eradicate *P. australis* completely, but the financial and environmental costs are high, as is the risk of reinvasion (Ailstock 2000). Consequently, management strategies should prioritize prevention over eradication.

Key preventive strategies are to halt propagule pressure from nearby sources or pathways (e.g. right-of-way that serve as invasion foci), address unfavorable conditions (for abiotic filtering), or restore native plant composition (for biotic resistance) if it has been recently disturbed. There is growing evidence that restoring native plant cover by sowing a mixture of seeds on bare ground can be an effective measure to slow or prevent some invasive plant growth and expansion (Kettenring and Adams 2011). This

approach raises many practical issues, including how to select, combine and determine the appropriate conditions for the species to be applied for the purposes of restoration. As the ultimate test of ecological theories (Ewel 1987), restoration may require us to develop a more complex understanding of invasion mechanisms. Ecological principles from community and invasion theories provide unique opportunities to guide community reassembly and create restoration practices that could control invasion (Shea and Chesson 2002, Zedler 2005, Funk et al. 2008). In particular, there is a critical gap of knowledge about the species-interaction mechanisms that underlie biotic resistance: how do plant functional group identity and diversity interactively work to resist invasion? How is such biotic resistance modulated by other factors, including abiotic constraint and/or propagule pressure? To date, these questions have not been explored in depth. New, advanced analytical tools, such as the diversity-interaction (Kirwan et al. 2009, Connolly et al. 2013) and structural equation models (Grace 2006, Grace et al. 2010) now enable testing of multiple alternative hypotheses about community reassembly mechanisms, and have great potential to enrich the discipline of ecology.

1.2. Research objectives and hypotheses

My PhD research goal was to determine the fundamental mechanisms underlying biotic resistance to invasion, based on community ecology and invasion theory. In terms of applications for invasive plant management, my aim was to identify highly invasion-

resistant plant(s) that could be re-established from applied seed mixtures to restore vegetation cover in disturbed areas at great risk of invasion by *Phragmites australis*. To achieve these goals, I used a synthetic approach combining (1) a functional framework, (2) experiments and (3) statistical modeling. Throughout my research, I used *Phragmites australis* invasion into wetlands as the main model to investigate invasion mechanisms. First, I used functional groups of wetland plants based on their trait dissimilarity to facilitate generalisation. Second, I designed and conducted several experiments in either wetland microcosms or a wetland basin in the field. Third, to understand the fundamental mechanisms of biotic resistance in relation to niche, I applied several statistical models (e.g., the diversity-interaction and structural equation models) to the experimental dataset, to analyse complex patterns of species interactions. The corresponding detailed hypotheses for each of the three main studies conducted as part of this research are presented below.

Study 1: Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass (Chapter 3)

In the first study, I investigated the biotic resistance of wetland plants to seedling establishment of *P. australis* in pot experiments. I assumed that certain kinds of plant species would be more resistant to invasion than others, based on their functional characteristics. In this regard, I hypothesized that (1) functional group identity of a species

would be a good predictor of its biotic resistance to *P. australis*. In addition, I hypothesized that (2) mixtures of species would be more invasion-resistant than monocultures. I tested several wetland plants by applying their seeds on bare wetland soils. This study made it possible to test the role of plants' functional traits and ecological niches in relation to biotic resistance to invasion.

Study 2: Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion (Chapter 4)

In the second study, I aimed to quantify the systematic interplay between biotic resistance and abiotic constraint and propagule pressure in determining invasion of *P. australis*. I modified water levels (as abiotic constraints) and/or changed seed-sowing density (propagule pressure) to evaluate how biotic resistance is modulated by these factors using structural equation models. First, in a species-environment experiment, I hypothesized that (1) biotic resistance to *P. australis* would be modulated by the way in which each wetland plant species responds to the abiotic constraint, while the direct effect of flooding would have consistent impact on *P. australis* seedling establishment. Second, in a follow-up propagule experiment, I aimed to determine whether (2) there is a threshold effect in propagule pressure on *P. australis* invasion and its interaction with sowing density of resident plants.

Study 3: Diversity reduces invasion through functional group interactions in plant community reassembly (Chapter 5)

I tested diversity-invasibility in a unique large-scale field experiment in a wetland basin with a heterogeneous environment. In addition to experimental seeding, the site was exposed to natural seed dispersal from surrounding meta-communities, including nearby mature *P. australis* stands. This study focused on functional group composition as well as biodiversity, and was therefore further diversified and more complex (but realistic) compared to the pot experiments. In addition, biotic resistance was tested against not only *P. australis* but also two other naturally-dispersed unsown species. A multi-model approach was used to select the best model(s) to explain and predict experimental data from among model candidates. The models' diversity-interaction parameters included functional group identity (or null identity effect) and interaction between functional group (or functional diversity or species diversity or null interaction).

Chapter 2 Literature review

In this chapter, I first review the key determinants of the course of invasion as discussed in the literature. I introduce several mechanisms that have been proposed to explain invasion success. I used the terms “invasion success” and “invasion outcome” alternately in this thesis acknowledging, however, that although “success” is widely used, it may be viewed by some as an unclear, subjective descriptor of restoration outcomes (Zedler 2007). Then, I explain why some of these are relevant for application in ecological restoration and invasive plant management. I present several case studies that have applied similar ecological principles to controlling invasive plants and compare the effectiveness of their approaches in reducing the invasion. Finally, I review characteristics of invasive species and use *Phragmites australis* as a model of invasive plants. I review its current status, invasion pathways and impacts on ecosystems. I conclude by identifying gaps in our current knowledge that the chapters to follow will help to fill, and the practical solutions that my research seeks to identify.

2.1. Key determinants of the invasion process

Biological invasion is defined as a process where a new species is recruited from outside of its native range (Lockwood et al. 2007). Figure 2-1 illustrates the multiple steps of the course of invasion (introduction, colonization, naturalization, spread, and

impact). The seedling in the colonization/establishment phase represents a critical window of opportunity for determining whether the introduced species will ultimately establish a self-sustaining population or not (Dietz and Edwards 2006, Van Kleunen and Johnson 2007b, Catford et al. 2009). This represents the most vulnerable stage for most invasive plants (Fraser and Karnezis 2005).

Recruitment of invaders depends mainly on three factors that together determine the outcome of the invasion - biotic resistance, abiotic constraints, and propagule pressure (Catford et al. 2009, Miller et al. 2013). Biotic resistance refers to the ability of species in a resident community to limit a biological invasion of exotic plants (Levine et al. 2004, Catford et al. 2009). Various components of a recipient community, including competitors, consumers and/or pathogens, can contribute to biotic resistance to invasion (Levine et al. 2004). This phenomenon has been well-documented in community ecology (Elton 1958, Fox 1987, Levine and D'Antonio 1999, Prieur-Richard et al. 2000, Pokorny et al. 2005, Fridley et al. 2007), and is central to our understanding of how communities at risk of invasion assemble after disturbances (Davis et al. 2000, Lindig-Cisneros and Zedler 2002c, de Blois et al. 2004, Simmons 2005, Iannone III and

Galatowitsch 2008, Reinhardt Adams and Galatowitsch 2008, Meiman et al. 2009, Perry et al. 2009).

Abiotic constraints refer to environmental conditions, stressors, or filters that can suppress recruitment of intolerant invaders (Gleason 1926, Weiher and Keddy 1995, Melbourne et al. 2007). For example, limited resources or climatic conditions can constitute abiotic constraints (Davis et al. 2000, Davis and Pelsor 2001). The outcome of strong abiotic filtering results in trait underdispersion and phylogenetic clustering during community reassembly (Procheş et al. 2008, Adler et al. 2013). Similarly, any disturbance event may release invaders from these abiotic constraints and can provide a critical window of invasion opportunity (Hobbs and Huenneke 1992).

Propagule pressure (1) a number of individual (propagules) that are released into a location (invasion quantity; defined as propagule size), (2) how often they are released (invasion frequency; defined as propagule number) (Lockwood et al. 2005), and (3) “number of species” released into a single location, defined as “colonization pressure”, a variant of propagule pressure (Lockwood et al. 2009). Although there are three variants of propagule pressure, I use the more generic term “propagule pressure” to describe the number of *P. australis* seeds per experimental unit (or sowing density) throughout my study. Propagule pressure has been identified as a key element in determining invasion

outcome (Lockwood et al. 2005). However, estimating the effect of propagule pressure is difficult, due to potential interactions with other factors (biotic resistance or abiotic constraints).

Results of field studies are not consistent with regard to the relative importance of each determinant (Thomsen et al. 2006b, Perelman et al. 2007). In some cases, propagule pressure has been found to overwhelmingly determine invasion outcome (Holle and Simberloff 2005). Other studies have reported that abiotic constraints (Von Holle 2005, Thomsen et al. 2006b) or biotic factors (Davies et al. 2011) predominantly controlled invasion. Recent evidence suggests it is unlikely that a single principle or mechanism governs the entire invasion process. Rather, biotic resistance, abiotic constraint and propagule pressure appear to interact with each other (Perelman et al. 2007).

Ecological resistance refers to the combined impacts of biotic resistance and abiotic constraints on invasion outcome (Holle and Simberloff 2005, Thomsen et al. 2006b).

Although this concept has not been used as frequently as biotic resistance, it is relevant to describe the dynamic between the two factors in determining invasion outcome (Perelman et al. 2007, Collinge et al. 2011). Likewise, understanding the invasion process requires a synthetic approach: evaluating not only the individual effect of each

factor, but also disentangling their interaction effects.

2.2. Mechanisms that are determinants in the invasion process

Several mechanisms have been proposed to explain biological invasion (Shea and Chesson 2002, Fridley et al. 2007, Sax et al. 2007, Funk et al. 2008, MacDougall et al. 2009), as summarized in Table 2-1. These mechanisms are not necessarily mutually exclusive, since several processes may work synergistically or in alternation, depending on context and scale (Pauchard and Shea 2006, Fridley et al. 2007).

Mechanisms of biotic resistance (individual effect)

The biotic resistance of each individual species can be explained by mechanisms of niche difference (e.g. limiting similarity) and fitness difference (e.g. competitive ability) between native and exotic species. Figure 2-2 illustrates how the relationships between these mechanisms determine the outcome of invasion in a single theoretical framework (MacDougall et al. 2009). The functional traits framework is useful for explaining how a species' niche and/or fitness determines invasion (Funk et al. 2008 Drenovsky, 2012 #1052). This mechanism is covered mostly in Chapter 3.

Limiting similarity (niche difference)

Limiting similarity, from classical competition theories (MacArthur and Levins 1967, Weltzin et al. 2003) postulates that there is a limit to the similarity in niche overlapping or resource use between recipient species and invading species. Functional traits are defined as the morpho-physio-phenological characteristics of a species (Cornelissen 2003, Violle et al. 2007). The functional traits framework positions a species in terms of niche and fitness (Funk et al. 2008, Drenovsky et al. 2012, Eisenhauer et al. 2013) and explains community assembly (McGill et al. 2006). According to this theory, an invading species will not establish where a recipient species occupies similar niches or traits (Funk et al. 2008). A functional group interpretation of the concept of limiting similarity can be also considered: the related Fox's assembly rule hypothesizes that the lack of a certain functional group in a resident community will make that community more susceptible to invasion by that particular functional group (Fox 1987, Von Holle and Simberloff 2004).

Competitive ability (fitness difference)

When niches overlap, the fitness difference between the resident species and the invader determines which one will be competitively excluded (MacDougall et al. 2009). Performance traits such as plant height (Gaudet and Keddy 1988), biomass (Gaudet and Keddy 1988, Lulow 2006, Rinella et al. 2007), plant cover (Gerhardt and Collinge 2003) or plant size (Schamp and Aarssen 2010) can be indicative of community-wide

fitness or induced biotic resistance. Biomass of resident communities has been identified as one of the best indicators of competitive ability (Gaudet and Keddy 1988) and level of biotic resistance (Lulow 2006). High biomass of resident species could reflect the way in which available resources are utilized and leaves less resources available for potential invaders.

Priority effect

Early emergence can be an important component of plant fitness (Verdú and Traveset 2005) and contribute to biotic resistance (Firn et al. 2010). Species that establish earlier and grow faster can benefit from a priority effect, which inhibits a subsequent invader from penetrating the community assembly (Mwangi et al. 2007). In community assembly, for instance, some annual plants grow faster, leading to a priority effect that can be expressed as 'first come, first served' (Young 2001, Fukami et al. 2005).

Mechanisms of biotic resistance (diversity effect)

Biotic resistance of multiple species is related to coexistence mechanisms among native species in a recipient community and their diversity effects on invaders. These mechanisms are discussed primarily in Chapter 5 (and partly in Chapter 3).

Vacant niches

The concept of vacant niche postulates that a species can establish in a habitat to fill a niche not previously occupied by a resident species. The Hutchinsonian niche concept (i.e., N-dimensional hypervolume) precludes this concept, because a niche cannot be defined without a species. Furthermore, the empirical evidence does not support the vacant niche concept, since niches are not saturated even in intact communities (Tilman 1997, Callaway and Maron 2006).

Diversity-resistance hypothesis (Niche partitioning)

The diversity-resistance hypothesis predicts a positive relationship between species diversity and biotic resistance (Elton 1958). Diverse communities have less unused niche space, thus preventing invasion (Funk et al. 2008, MacDougall et al. 2009). The more species are present in a resident community, the more likely a species' niche overlaps with that of invaders, which increases competition intensity. Niche partitioning or trait complementarity can increase biotic resistance. Niche partitioning can be demonstrated empirically by increasing the number of neighboring plants (Kennedy et al. 2002), canopy complexity (Lindig-Cisneros and Zedler 2002c) or resource uptake partitioning (e.g., soil nitrogen forms) (Booth et al. 2003, Ashton et al. 2010, Frankow-Lindberg 2012). Furthermore, trait complementarity (e.g., a combination of species that are functionally very different from each other) can help maintain both community stability and resistance (Fargione and Tilman 2005). The related hypothesis of

insurance effect states that diversity increases community-wide stability under a fluctuating or heterogeneous environment (Ives et al. 2000, Loreau et al. 2001, Tilman et al. 2006), with a potential scale effect in the field (Balvanera et al. 2006, Fridley et al. 2007).

The scale dependence of the diversity–resistance relationship is recognized as the “invasion paradox” (Fridley et al. 2007). Small-scale experimental studies generally support the diversity-resistance hypothesis (Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Dukes 2002, Kennedy et al. 2002, Rinella et al. 2007, Frankow-Lindberg et al. 2009a, Frankow-Lindberg 2012), as do competition-based models (Case 1990). It is assumed that diverse communities with a broad range of niches offer invaders fewer available niches. On the other hand, large-scale observational studies that directly investigated the effect of scale (Levine 2000, Brown and Peet 2003) have reported opposite patterns (Stohlgren et al. 1999, Stohlgren et al. 2003), as do statistical models that either consider both competition and resource available across communities (Byers and Noonburg 2003) or assume null species interaction (Fridley et al. 2004). This scale-dependency is now widely recognized among invasion ecologists. Figure 2-3 shows how these apparently opposing patterns can be reconciled. Species-rich communities are more resistant to invasion than species-poor communities, while species-rich ecosystems and regions are likely to be hotspots not only for native

species but also for exotic species (Fridley et al. 2007). The latter may even be better adapted to the environment than the former (Shea and Chesson 2002, Callaway and Maron 2006, Verhoeven et al. 2009).

Functional diversity; trait complementarity

If species' traits are well-dispersed over available niche space, the entire community may be resistant to potential invaders (Funk et al. 2008). In this regard, functional group richness (or functional diversity based on trait complementarity) could be a more direct indication of invasion resistance than species diversity (Symstad 2000, Pokorny et al. 2005). Figure 2-4 summarizes a hypothesis about the role of functional diversity in the relationship between species richness and invasion resistance. According to some hypotheses, all types of functional groups are of equal importance (Pokorny et al. 2005, Rinella et al. 2007), but others predict that functional group composition (e.g. ratio of each functional group) can be as important as functional diversity (Tilman et al. 1997, Prieur-Richard et al. 2000).

Partitioning diversity effect

Diversity effect, recognized as one of the main drivers of biotic resistance to invasion, can be divided into "complementarity diversity effect" and "selection effect" (Loreau and Hector 2001). Complementarity diversity effect can be significant if resource partitioning,

or positive interaction between species, contributes most to net diversity effect (Levine and D'Antonio 1999, Kennedy et al. 2002, Levine et al. 2004). With regard to the concept of niche, theories of diversity-resistance state that diverse communities have less unused niche space, thereby preventing invasion (Kennedy et al. 2002, MacDougall et al. 2009). Niche partitioning can be the result of an increase in number of neighboring plants (Kennedy et al. 2002), canopy complexity (Lindig-Cisneros and Zedler 2002a), or resource uptake (Booth et al. 2003, Frankow-Lindberg 2012). A related theory of fluctuating resource availability postulates that invaders will take advantage of short-term increases in available resources that have remained unused by local communities (Davis et al. 2000). Functional traits of species are related to their niche and fitness (McGill et al. 2006), and therefore, if species' traits are well dispersed over available niche space in a community, fewer resources remain available for potential invaders (Funk et al. 2008). In this regard, functional group diversity could be more directly indicative of a complementarity diversity effect on invasion resistance than species diversity (Symstad 2000, Pokorny et al. 2005; but see also Prieur-Richard et al. 2000). A selection (or sampling) effect, on the other hand, can be significant if certain species present by chance in a community essentially influences the diversity effect (van Ruijven et al. 2003, Emery and Gross 2007). Growing empirical evidence indicates that both complementarity and selection effects can contribute to a net diversity effect

on invasion resistance (Fargione and Tilman 2005, Frankow-Lindberg et al. 2009e); little is known, however, about their relative impact on a diversity effect.

Mechanisms of abiotic factors

Environmental constraint (abiotic filtering) hypothesis

Abiotic constraints suppress intolerant species, including invaders that serve as environmental filters (Gleason 1926, Weiher and Keddy 1995, Melbourne et al. 2007). Field studies have also shown that abiotic constraints play a significant role in determining invasibility in heterogeneous flooded environments (Gerhardt and Collinge 2003, Collinge et al. 2011), sediment salinity (Dethier and Hacker 2005), soil nutrients (Goldstein and Suding 2013) and overstory tree composition (Von Holle 2005). A strong environmental filtering process leads to trait underdispersion and phylogenetic clustering during community reassembly (Procheş et al. 2008, Adler et al. 2013).

Fluctuating resource availability

The fluctuating resource availability theory suggests that plant communities become more vulnerable to invasion if the amount of unused community resources (i.e., resource availability) increases (Davis et al. 2000). According to this synthetic theory, a combination of abiotic and biotic factors determines resource availability. When the supply of resources (abiotic factor) is controlled, or if resource acquisition (biotic factor)

by recipient communities increases, invasion will occur less frequently. The notion that competition is less important in recently disturbed environments where resident plants are not sequestering all available resources underlies this theory (Davis et al. 1998; Grime 1974, 1988), which has been the subject of much debate and is supported by some empirical evidence (Davis and Pelsor 2001, Iannone III and Galatowitsch 2008, Frankow-Lindberg 2012). Any disturbance event that changes abiotic constraints, from extreme climatic events (Collinge et al. 2011, Goldstein and Suding 2013) to increased resource availability (Davis et al. 2000, Davis and Pelsor 2001), can trigger an invasion.

Interplay between abiotic constraints and biotic resistance

The intensity of abiotic constraints can affect the relative importance of abiotic and biotic factors in resisting invasion (Gerhardt and Collinge 2003). In stressful and harsh environments, abiotic constraints may entirely determine the fate of invaders (Dethier and Hacker 2005, Wang et al. 2006f, Chytrý et al. 2008). In benign or intermediate conditions, in contrast, biotic resistance becomes as important as abiotic constraints (Naeem et al. 2000, Gerhardt and Collinge 2003, Thomsen et al. 2006a, Thomsen et al. 2006b, Perelman et al. 2007). Furthermore, these factors may be correlated to each other in a systematic rather than simply linear manner (Perelman et al. 2007, Collinge et al. 2011). Determining the causal relationship underlying connections among multiple factors should improve our understanding of the invasion process at the scale of the

whole system. Recent advances in modeling analysis such as structural equation models (Grace et al. 2010) enable us to verify hypotheses of interaction and casual relationship in a variety of ecosystems (Whalen et al. 2012). However, it has not been applied yet in testing different models of invasion prediction. Figure 2-5 illustrates my hypothesis of causal relationships among factors, which aims to systemize the invasion process. This conceptual diagram is also used to build structural equation models in Study 2 (Chapter 4).

Mechanisms of propagule pressure

The role of propagule pressure in the invasion process is straightforward: 'the more you introduce, the more you get' (Lockwood et al. 2009). Propagule pressure alone explained 56% of the variance in exotic richness in one case study (Lonsdale 1999). The rate or extent of an invasion (abundance of invaders) in the field is often a poor indicator of actual propagule pressure (Eschtruth and Battles 2011) because environmental heterogeneity and community invasibility can compromise invasion outcome from propagule pressure. In addition, different dispersal mechanisms may predominate, depending on the scale (Pauchard and Shea 2006).

There has also been considerable interest in the shape of the dose-response curve (relationship between propagule numbers and invasion), yet little is known about this

relationship (Lockwood et al. 2005). It is uncertain whether invasion results in consistent or marginal benefits from propagule pressure, or whether saturation occurs beyond a certain threshold (Lockwood et al. 2005). A net balance between “propagule pressure” and “extinction rate” may determine invasion outcome in the end (Lonsdale 1999). Demographic stochasticity may result in a greater extinction rate (i.e., allee effect) until a population reaches a certain level of genetic diversity (Gertzen et al. 2011, Britton and Gozlan 2013).

The extent of the invasion (current distribution of invaded species) in the field poorly reflects *in situ* propagule pressure (Eschtruth and Battles 2011, Miller et al. 2013). Rather, it suggests habitat suitability at a given level of propagule pressure. There is significant interaction between abiotic constraints and propagule pressure, which suggests that alleviating abiotic constraint/stress can help more individuals establish at a given propagule pressure (Thomsen et al. 2006b, Adler et al. 2013).

Characteristics of invaders

What make species like *P. australis* invaders? This is an important question, particularly for prioritizing management efforts. Certain differences in plant characteristics (or functional traits) between alien and native species can be used to evaluate potential invasiveness (Pyšek and Richardson 2007, Van Kleunen et al. 2010) and explain

invasion outcome (Herborg et al. 2007, Drenovsky et al. 2012, Leung et al. 2012). For instance, plants with short life cycles that produce many seeds have greater potential to spread out, exhibiting the 'live-fast, die-young' trait syndrome (Franco and Silvertown 1996). In addition to biological traits, non-biological plant characteristics such as native range, human uses and introduction year can also be important (Lavoie et al. 2013). Quantifying the relationship between plant characteristics and invasiveness can contribute to the development of a management tool to assess invasion risk (Leung et al. 2012). Table 2-2 summarizes literature reviews on the relationship between invaders' characteristics and their invasiveness. In a related research project to develop a tool to predict invasion risk under climate change and to prioritize management efforts (de Blois et al. 2013), *P. australis* ranked second on a combined index of both invasiveness and climate-based habitat suitability among a total of 38 widespread/harmful invasive plants in North America.

2.3. Ecological applications to control invasive plants

In this section, I first present conventional eradication methods, Then, I will introduce alternative approaches of plant community restoration to prevent invasion, along with empirical evidences. Lastly, I discuss how mechanisms (discussed as the above) are related to plant restoration practices.

Conventional eradication methods

Mechanical, chemical, and biological control can be used to eradicate invasive plants.

Mechanical control commonly involves mowing and/or burning invasive plant stands.

Mowing is usually not very effective in controlling exotic *P. australis* (Ailstock et al. 2000) and must often be repeated to ensure effective control (Farnsworth and Meyerson 1999, Güsewell et al. 2000), in large part because most belowground parts (e.g., rhizomes) remain unscathed (Güsewell et al. 2000). Burning is usually not very effective for the same reason (Thompson and Shay 1989, Rolletschek et al. 2000). For instance, after three to four years, *P. australis* re-invaded sites on which stands had been controlled by mowing or burning (Farnsworth and Meyerson 1999, Warren et al. 2001). Solarization (i.e. covering with sheets of black plastic) has proved to be an effective measure against other exotic species (Marushia and Allen 2011), but it is also one of the most expensive methods and almost impossible to apply over large areas.

In chemical control, an herbicide is applied on leaves or stems to kill entire invasive plant individuals (roots are affected as well). For instance, in the United States, spraying herbicide (e.g. Glyphosate or Imazapyr) is a popular method for eradicating *P. australis* (Westerdahl and Getsinger 1988, Farnsworth and Meyerson 1999, Mozdzer et al. 2008, Hazelton et al. 2014). Herbicide application or a combination of herbicide and burning has been shown to be effective in both reducing the abundance of *Phragmites* and

increasing native plant diversity (Ailstock et al. 2000). Chemical control can be most effective when applied for several years, although there are possible negative impacts of the herbicide on the ecosystem. The use of herbicides is often prohibited in wetlands, for instance, in Quebec (Lavoie et al. 2003).

Biological control utilizes a bio-agent (e.g., natural enemy of the plant, such as an herbivore). The effectiveness of this approach has been tested and well demonstrated against *Lythrum salicaria* (Purple Loosestrife) (Malecki et al. 1993). A case study which integrated both biological control and eradication resulted in effective management of *Persicaria perfoliata* (introduced annual Mile-a-minute weed) (Cutting and Hough-Goldstein 2013). In the case of *P. australis*, a bio-agent is still in development (personal communication with a leading scientist in this field, Dr. Bernd Blossey, Cornell University). Since *P. australis* is an exotic species in North America, only few of its natural “enemies” exist here; this may suggest potential avenues to explore in the future (Tewksbury et al. 2002). There are genuine risks of harmful side-effects for entire ecosystems, of introducing yet another exotic species. In conclusion, biotic control measures are not a viable option for *P. australis* at this time.

Overall, past and current management strategies have focused mainly on eradication – e.g. how efficiently a spray herbicide will be for killing a plant, without ecological

consideration (Kettenring and Adams 2011). To ensure zero invasion, one should repeatedly apply eradication methods for several years and combine this with follow-up monitoring (Blossey 1999). Arguably, it is almost impossible to block every possible invasion pathway, or kill every remaining propagule without severe disturbance of the ecosystem. Conventional control measures (mechanical and chemical) are usually expensive and environmentally damaging; they may also promote reinvasion, by disturbing sites (Simmons 2005). More importantly, killing invasive plants does not guarantee native plant communities' full recovery. Eradication of invasive plants was followed by an increase in native diversity (Dodson and Fiedler 2006, Middleton et al. 2010, Marushia and Allen 2011, Thomsen et al. 2012). However, natural recovery processes can be slow (due to lack of propagules), thus providing equal opportunity to potential invaders.

Ecological restoration: creating vegetation cover in bare ground

Ecological resistance, the combined impacts of biotic resistance and abiotic constraints on invasion outcome, can guide the restoration of native communities and/or protect them from invaders (Zedler 2000, Hobbs and Richardson 2010b). For instance, meta-analyses on this subject show that implementation of a plant cover can interfere with invasion while achieving restoration goals (de Blois et al. 2004, Cutting and Hough-Goldstein 2013).

Benefits of plant restoration compared to conventional control methods

The fundamental problem of the above-mentioned eradication methods is that removal of plants inevitably causes disturbance (e.g., bare ground), which can trigger reinvasion (Iannone III and Galatowitsch 2008). The main advantages of an ecological restoration approach are that it (1) is self-regenerative, so repeated application is unnecessary; (2) poses less of a threat to resident, native or desired plants, and (3) avoids disturbance, which can trigger reinvasion (Simmons 2005). For these reasons, restoring native plant covers could represent an alternative and innovative technique for protecting native communities from invasion or restoring them. Nonetheless, invasive plant control programs usually do not evaluate the role of native revegetation following removal (Kettenring and Adams 2011). To date, most experimental research to test plant restoration has shown mixed results in terms of the effectiveness of these methods for controlling invasion.

Case studies of plant restorations to control invasion

Empirical studies that have attempted to control invasion by restoring biotic resistance have achieved some positive results while encountering some limitations. Table 2-3 summarizes results of research projects that engaged in plant restoration to control invasive plants. Too little information is available to guide plant restoration, particularly

at the community-level and in regard to invasive plant management (Hazelton et al. 2014).

To date, only few case studies have applied biotic resistance to control *P. australis* invasion. Two experimental studies were conducted in salt marshes (Wang et al. 2006a, Peter and Burdick 2010). In a field experiment on transplanting four native halophytes inhibited about 60% of shoot growth of *P. australis* established from rhizome (Peter and Burdick 2010). The results of this experiment supported diversity effects (mixtures of four species were more resistant than a single species); a strong selection effect was also found for one species (e.g. *Spartina alterniflora*). In another experiment, a *P. australis*-dominated salt marsh was cleared and restored with native plants by planting or tissue culture regenerants (Wang et al. 2006a); some restored plants (e.g. *Spartina patens*) effectively controlled *P. australis*. *Spartina* sp. thus seems to be a good candidate for control of *P. australis* in salt marsh restoration.

Sowing seeds of native plants at high density (150,000 seeds m⁻²) suppressed *Phalaris arundinacea* (reed canarygrass), but failed to stop recruitment at propagule pressure as little as 10 seeds m⁻² (Reinhardt Adams and Galatowitsch 2008). In other case studies, the most dense plant cover resulting from seed mixtures of six native species and a matrix of *Glyceria striata* significantly hindered expansion of *P. arundinacea* (Lindig-

Cisneros and Zedler 2002c). Creating a crop plant cover on bare soil (thereby lowering light availability) controlled 89% of invasion by *P. arundinacea*, but also suppressed desired species (restoration target communities) by 57% (Iannone III and Galatowitsch 2008). In the same experiment, applying sawdust (high C:N ratio) lowered available nitrogen in soil and delayed and decreased invasion by 59%, while not affecting desired target communities.

In a field experiment with *Centaurea diffusa* (knapweeds), a canopy cover consisting of mixed-grass was treated with different opening sizes (i.e., interspaces among the bases of established native plants) (Meiman et al. 2009). *C. diffusa* seedling establishment was greater in openings sizes of 5 and 15 cm than in opening size of 0 cm (treatment). In another field experiment, the highest sowing density of native Indian blanket (*Gaillardia pulchella*) resulted in an 83% reduction of invasion by *Rapistrum rugosum* (annual bastard cabbage) (Simmons 2005).

Sowing both native seeds and a biocontrol weevil (*Rhinoncomimus latipes*) reduced *Rapistrum rugosum* (annual bastard cabbage) invasion by 75% (Cutting and Hough-Goldstein 2013). Synergetic effects (described as 'additional effect' by the authors) were observed from combining the plant's natural enemy and competitors.

In a case where multiple invaders were present among *Cardaria draba*, *Cirsium arvense*, *Bromus tectorum*, and *Bromus japonicas*, some of the annual cover crops tested (Ragweed and Sunflower) controlled less than 50% of invasion by *Cirsium arvense*, and *Cardaria draba*, and facilitated invasion by other species (*Bromus tectorum*, *Bromus japonicas*) (Perry et al. 2009). The crop cover plants were not very effective in controlling *P. arundinacea*, either.

Community compositions including two densities of monoculture and all possible mixtures of *Schoenoplectus americanus* (a sedge), *Baccharis salicifolia* (a shrub), and *Salix gooddingii* (a tree) were tested to control *Arundo donax* (a giant weed) in a field experiment on riverine restoration (Quinn and Holt 2009). The lowest level of invasion was observed in a mixture of a shrub and a tree, but positive effects experienced in the first year did not persist in the second year.

Limitations of plant restoration

While some empirical evidence suggests that plant restoration enhances biotic resistance, this alternative management approach also has some limitations. Depending on seed mixture, site conditions and target invaders, the effectiveness of plant restoration is highly variable, from a low of less than 50% of invasion to a high of more than 90% of invasion in some cases. In most field studies, few invading individuals

survived after all phases of restoration had been completed. In conclusion, biotic resistance alone does not guarantee complete suppression of invasion (Levine et al. 2004). Rather, biotic resistance can contribute to constraining invasion by reducing invaders abundance (Levine et al. 2004) or determining the identity of invaders at regional scale (Fargione et al. 2003, Davies et al. 2011).

Ecological control and relevant mechanisms

To restore invasion-resistant plant communities

Among the various theories and mechanisms described above, two mechanisms are particularly relevant for controlling invasive plants in protected and disturbed areas in the context of management and restoration of native communities. These are (1) functional-traits-based biotic resistance (limiting similarity or competitive ability) and (2) diversity-resistance (niche partitioning and trait complementarity effect). The first mechanism is related primarily to niche difference (e.g. limiting similarity) and/or fitness difference underlying competitive exclusion between native and exotic species (MacDougall et al. 2009). The second mechanism is related to niche partitioning and/or trait complementarity (functional diversity), and includes patterns of coexistence among native species and the diversity of their effects on exotic species. A diverse community can also uptake more resources and leave less resources for invaders. Finally, it is very important to simultaneously quantify several mechanisms and evaluate their relative

importance in heterogeneous restored plant communities (covered in Chapters 3 and 5).

Toward “adaptive” restoration

To extend the context in which these mechanisms can have an ecological application, it is also important to understand how biotic resistance is modulated by (3) abiotic constraints (environmental filtering) and/or resource availability and (4) propagule pressure and species recruitment rate. Abiotic constraint affects recipient plants' establishment and growth (fitness), thus assisting or precluding their resistance to invasion. The relationship between propagule pressure (seed density) and invasion outcome can be used to estimate invasion risk given propagule pressure, and to calculate effective levels at which to sow native seeds (both mechanisms are covered in Chapter 4).

2.4. *Phragmites australis* as a model invasive plant

Invasion status of *P. australis*

Phragmites australis Trin. ex Steud is a cosmopolitan tall grass plant, found in both freshwater and brackish wetland ecosystems around the world (Haslam 1972). In North America, the exotic genotype of *P. australis* was introduced from Eurasia over a century ago and has gradually spread throughout the continent (Saltonstall 2002, Meyerson et

al. 2009, Meyerson et al. 2010). Its invasion and expansion is associated with the exotic genotype (haplotype M) (Rice et al. 2000, Saltonstall 2002, Howard et al. 2008). There is recent direct evidence for hybridization with a native genotype (Meyerson et al. 2010). More than 95% of common reed colonies in Quebec are dominated by the exotic *P. australis* (Lelong et al. 2007), which is more typical of disturbed habitats such as roadsides ditches (Taddeo and Blois 2012).

Exotic *P. australis* may be one of the most pervasive and persistent invasive plants in North American wetland ecosystems once it reaches maturity, forming tall dense stands 3-4 years after seedling establishment. These extensive mono-specific stands (Cronk and Fennessy 2001, Zedler and Kercher 2004) average 30 to 400 shoots m⁻², and shoots can reach 2~4 m in height (Haslam 1972). The plant's density and height contribute to its dominance, as it occupies the maximum available space and prevents light penetration, providing very little opportunity for other species to inhabit an area (Haslam 1971a). A dense network of rhizomatous reserves may extend up to 2 m either horizontally or vertically, providing the plant with the ability to persist under adverse conditions (Haslam 1971c). *P. australis* has wide genetic and phenotypic plasticity, as well as strong tolerance to disturbance and herbivores (Engloner 2009, Kettenring et al. 2011).

Invasion pathways

It was originally believed that *P. australis* invades mostly through vegetative reproduction. Patches of the plant can expand clonally through vegetative reproduction, using rhizomes (underground) and shoot runners or stolons (above ground or below the water surface) to produce new stalks that take root. However, the estimated growth rate of patches is as low as about 1 m per year (Lavoie 2008). Older studies reported more variable measures: 10 m per year (Haslam 1972), and about 3 to 22 m based on analysis of aerial photos (Haslam 1972). Thus, “clonal expansion” alone cannot explain how exotic *P. australis* spread out all across North America.

One possible pathway of *P. australis* invasion is through long distance transport of rhizome or stolon fragments. Machinery work such as ditch digging, plowing, transport and deposit of rhizome-filled soil can unintentionally result in dispersal (Keller 2000a, Bart and Hartman 2003). Low genetic variability in some patches of *P. australis* supports the hypothesis of dispersal through vegetative means (Keller 2000a). In another observational study along a highway in Quebec, physical and biological characteristics of roadsides were good indicator for the presence and absence of *P. australis* stands (Albert et al. 2013). While there is no direct evidence yet to support this pathway, circumstantial evidence and field observations are beginning to emerge.

Seed dispersal may be the main source of invasion over long distances (Lockwood et al. 2005, Lockwood et al. 2009). New evidence also suggests that seed dispersal is a significant invasion strategy for *P. australis*. Belzile et al. (2010) reported great genetic variation among *P. australis* stands along Lake Saint-François (an area of about 51 km²) in Quebec. They found 134 different genotypes in 345 visually distinct patches of the plant. Another study observed that genetic distance is correlated to geographical distance among *P. australis* stands in China's Yellow River delta (Guo et al. 2003). A recent field survey in Quebec found *in-situ* seedling establishment of *P. australis* (Brisson et al. 2008). Analysis of historical aerial photos has revealed that *P. australis* colonizes first over long distances, presumably by seeds, and then spreads gradually to nearby sites by vegetative means (Maheu-Giroux and de Blois 2005). Spatial autocorrelation analysis of microsatellite photos of 189 individuals showed that 18% of dispersal is associated with river flow, whereas 38 % is driven by wind in the Czech Republic (Fér and Hroudová 2009). The same study found that seeds can disperse up to about 10 km. This body of evidence clearly shows that *P. australis* can invade through seed dispersal, mostly in the early phase of invasion.

Propagule pressure

Propagule pressure from *P. australis* is thought to vary, depending on several factors including distance from a source (Langdon et al. 2010). A single flowering shoot of *P.*

australis produces on average 1509 (\pm 933) seeds (Coops and Velde 1995). Many studies about seed viability report good germination of *P. australis* in an experimental setting (Maheu-Giroux and de Blois 2007, Saltonstall and Court Stevenson 2007, Meyerson et al. 2009, Meyerson et al. 2010). Field tests report very low or no seed viability (Haslam 1971c, Gervais et al. 1993), but seed germination rates are highly variable and dependent on site conditions (Kettenring et al. 2011).

Human disturbance

As is the case for many other invasive plants, disturbance facilitates invasion by *P. australis*. In a field experiment in a salt marsh, disturbance that enriched nutrients and removed native competitors promoted its invasion (Minchinton and Bertness 2003). Any human activity that disperses seeds, buries rhizome fragments, lowers water level or salinity increases chances of invasion (Bart et al. 2006). At a landscape scale, occurrence of *P. australis* has been shown to coincide with human land use in Chesapeake Bay (King et al. 2007, Chambers et al. 2008) and in New England salt marshes (Silliman and Bertness 2004).

Establishment and growth condition

P. australis seeds require at least 2.5 % oxygen concentration to germinate (Wijte and Gallagher 1996b, Engloner 2009). Seedlings need bare ground and humid conditions to

establish (Alvarez et al. 2005). One study found that when submerged, seedling growth was not significant, and 18.7% of 40-day-old seedlings were dead (Mauchamp et al. 2001). It is also thought that *P. australis* invasion progresses under climate change. For example, *P. australis* seeds germinate better and faster at high (15-20 °C) than at low temperatures (10°C) (Gorai et al. 2006).

Once established, *P. australis* tolerates a wide range of environmental conditions, including changing water levels (a range of about -50 cm to 100 cm) and salinity levels (as high as 30 ppm), which contributes to its invasiveness (Shay and Shay 1986, Cook 1996, Wijte and Gallagher 1996b, Wijte and Gallagher 1996a). The plant is not well-adapted to areas that remain deeply flooded (e.g. below 1 to 1.5 m) for a period of time (100 days). Nor does *P. australis* survive well where the water table is high for more than 100 days during the growing season (Shay and Shay 1986). In another instance, stands of *P. australis* retreated when water level increased along the Saint Lawrence River in Quebec (Hudon et al. 2005). Its rhizome fragments have much less tolerance to remaining submerged than does the mature plant (Amsberry et al. 2000).

Exotic *P. australis* grows much better in nutrient-rich conditions than other plants (Romero et al. 1999, Minchinton and Bertness 2003), and also better than native *P. australis* (Saltonstall and Court Stevenson 2007). When nutrients are abundant, *P.*

australis increases the aboveground structures it uses to spread (invests more in competition and reproduction), rather than in belowground structures used for nutrient uptake (because it can already ensure survival) (Minchinton and Bertness 2003). However, *P. australis* does not have fungal endophytes; therefore, it does not have the ability to fix N (Lambert and Casagrande 2006). A case study of *P. australis* planted in combination with *Spartina pectinata* showed that *P. australis* benefits more than the other species from nitrogen-rich soil (Rickey and Anderson 2004). Other field studies on a Swiss plateau, in Britain and in a greenhouse experiment also proved that the spread and growth of *P. australis* are positively related to soil nutrients content (Haslam 1971a, Güsewell and Klotzli 1998, Ravit et al. 2007).

Species can either maintain fitness in unfavourable conditions (Jack-of-all-trades) or increase their fitness in favourable conditions (master-of-some), but invasive plants like *P. australis* may have both abilities (Ailstock 2000, Richards et al. 2006, Mozdzer and Megonigal 2012). For instance, with higher chloroplast concentrations and photosynthetic rates than native wetland vegetation (Mozdzer 2005), it responds positively to elevated CO₂ and N (Hazelton et al. 2014).

Impacts on ecosystem

The negative impacts of *P. australis* have been demonstrated for several aspects of invaded ecosystems. First, in regard to native plant and animal species, several studies have reported rapid and aggressive replacement of native and diverse communities with mono-specific *P. australis* stands and a consequent sharp decrease in local native diversity in freshwater wetlands (Farnsworth and Meyerson 1999, Ailstock et al. 2000, Keller 2000c, Meyerson et al. 2000, Lavoie et al. 2003), tidal blackish wetlands (Amsberry et al. 2000, Meyerson et al. 2000, Silliman and Bertness 2004) and old fields (Stalter and Baden 1994, Byun et al. 2008). Dense monotypic stands provide unsuitable or less-preferred food and habitat for waterfowl and other wildlife (Roman et al. 1984, Thompson and Shay 1989, Chambers et al. 1999, Zedler and Kercher 2004), including aquatic benthic invertebrates (Roman et al. 1984, Wijte and Gallagher 1996b).

Second, *P. australis* alters habitat structure and biogeochemical process in its own favor (engineering species). For instance, *P. australis* can alter soil topology, increasing sedimentation through litter from its organic matter production, which results in an increase in ground elevation in marshland (Rooth et al. 2003). *P. australis* also fills in tidal creeks, as its roots anchor sediment (Zedler and Kercher 2004). Increased production in the ecosystem alters food chain, which in turn disturb the balance between organisms and biogeochemical processes. For instance, *P. australis* has great impact on soil nutrient cycling (Ehrenfeld 2003): compared to native plants, it has higher

plant biomass and NPP (net primary productivity); a higher decomposition rate of leaves; less extractable soil nitrogen compared to blackish marsh plants; greater nitrification and lower pH (Ehrenfeld 2003). The impact of *P. australis* on wetland soil environments is typical of invasive plants, although one study (Weis and Weis 2003) has argued that detritus from *P. australis* provides more favorable conditions than *Spartina alterniflora* in salt marshes for certain biota such as benthic biota and nekton .

Third, *P. australis* is generally viewed as a nuisance species for human activities as well. The plant invades and creates dense colonies in agricultural ditches, impeding drainage. Due to its high biomass, it is also combustible, so it may represent a fire hazard to nearby buildings or utility poles (Personal communication, Jacques Dextraze, Ducks Unlimited, Canada). Overall, *P. australis* currently represents one of the major threats to the conservation of wetland ecosystem functions and integrity.

Windows of invasion control opportunities

The critical moment of opportunity to control *P. australis* invasion is when its seeds arrive on a site with strong competitors already present in recipient communities, or with conditions unfavorable to it (e.g., flooded), both of which can prevent its seedlings from establishing. Seedlings that fail to reach the critical size (or height) by the end of the first growing season are unlikely to survive their first winter (Haslam 1975, Weisner and

Ekstam 1993). Therefore, detection and monitoring of *P. australis* at the initial stage of invasion, before it has established an underground rhizome network, is critical to control/eradication efforts (Maheu-Giroux and de Blois 2005, Saltonstall and Court Stevenson 2007). Moreover, this supports the overriding benefit of a preventive strategy, based on knowledge of *P. australis* characteristics and behavior (Ailstock et al. 2000, Keller 2000c).

2.5. Synthesis and relevant questions for invasive plant management and ecological restoration

Ecological principles and knowledge about invasion mechanisms can guide plant restoration that aims to control invasive plants. For instance, understanding mechanisms of biotic resistance can guide species selection and combination toward strong biotic resistance. Empirical studies to test the effectiveness of this approach show both potential and limitations. Applicable knowledge is required, however, and few studies have tested the multiple mechanisms that control invasive species simultaneously. Our model invasive plant, *P. australis*, is imposing a serious management challenge. Most conventional eradication methods are ineffective against this persistent plant. There is some empirical evidence to support the effectiveness of the plant restoration method for preventing the spread of such invasive plants.

To efficiently control and manage this persistent plant and other invaders, one may need to take into account multiple mechanisms of ecological resistance in developing a comprehensive management approach. To illustrate such an approach, we simulated a situation where high invasion risk is expected in disturbed areas (no vegetation cover/exposed bare ground), and restored a plant cover by sowing seeds of wetland species to evaluate biotic resistance mechanisms. This raises the following research questions for ecological restoration:

- What kind of species will resist most to invasion?

: covered primarily in **Chapter 3**. Plant functional group and biotic resistance.

One should consider site conditions and, if possible, adjust community composition for restoration accordingly based on knowledge of interactions among determinants. If the site is under high propagule pressure, abiotic conditions may be manipulated in addition to biotic resistance to suppress invasion. For instance, *P. australis* does not establish well under flooding, while other wetland plants may favor flooded conditions.

Furthermore, seed density for restoration can be adjusted by estimating propagule pressure at a single location. This raises the following research question:

- How does biotic resistance interact with abiotic constraints and propagule pressure?

This is covered primarily in **Chapter 4**. Biotic resistance interacts with abiotic constraint and propagule pressure.

In a situation where an invasive plant has already invaded and created dense mono-specific stands, applying eradication methods will be inevitable and necessary. Any eradication treatments should be applied carefully, with the aim of generating as little disturbance as possible (Dodson and Fiedler 2006). It should be followed by plant restoration so that desired species immediately occupy disturbed areas, thereby preventing reinvasion (Bakker and Wilson 2004, Iannone III and Galatowitsch 2008, Cutting and Hough-Goldstein 2013). I created an experimental plant community reassembly in a *P. australis*-dominated wetland basin. After eradication of *P. australis* stands, I applied seed mixtures, varying the number of species and functional group composition.

This poses the following research question:

- Which plant communities restored from applied seed mixtures most restrain recruitment of invading species under field conditions?

This is covered mostly in **Chapter 5**. Diversity-invasibility and functional group interactions and also partly in Chapter 3.

In the final chapter of discussion and conclusion, I synthesize the main results of each chapter and discuss implications for invasive plant management using plant restoration practices.

2.6. Tables

Table 2-1: Hypotheses about mechanisms of invasion determinants

Hypothesis of mechanism	Prediction	Evidence / Examples	Related hypothesis & additional remarks
<u>Biotic resistance</u>			
<u>(individual)</u>			
Limiting similarity (MacArthur and Levins 1967, Funk et al. 2008)	There is a finite limit of coexisting species in similar niches/ traits	A meta-analysis suggests only a limited role in invasion (Price and Pärtel 2013), e.g., support for forb invader, but not for grass invader	Functional traits (Funk et al. 2008); Fox's assembly rule: a functional group resists invader in same group
Competitive ability (fitness advantage) (MacDougall et al. 2009)	Competitive species are most resistant to invasion	Plant performance traits related with plant competitive ability (Gaudet and Keddy 1988)	Species with superior traits are most resistant (Kunstler et al. 2012)
Priority effect	Early emergence favors native over invader (early colonizers are resistant)	Supported over functional similarity (Mwangi et al. 2007, Finn et al. 2010); see also (Godoy and Levine 2013)	Priority effect (first come, first served)
<u>Biotic resistance</u>			
<u>(diversity)</u>			
Vacant niches (Stachowicz and Tilman 2005)	Invasion occurs where niche space is not occupied by species	Not supported by an experiment; niches in native communities are unsaturated (Tilman 1997)	Niche cannot be defined without a species in Hutchinsonian view
Diversity-resistance (Elton 1958)	More diverse communities are less invisible (via niche	Supportive experiments (Levine 2000, Kennedy et al.	Partitioning resource uptake (Booth et al. 2003)

	partitioning)	2002, Tilman et al. 2006); contrary patterns at regional scales (Stohlgren et al. 2003)	Both complementarity and selection effects matter (Fargione and Tilman 2005)
Functional diversity-resistance (Funk et al. 2008)	Functional diversity resists invasion via trait complementarity	Supportive experiments (Symstad 2000, Pokorny et al. 2005)	Functional diversity-ecosystem functions (Tilman et al. 1997); Functional composition matters (Prieur-Richard et al. 2000)
<u>Abiotic constraints</u>			
Environmental constraints hypothesis (=abiotic filtering)	Stressful or extreme environment filters out intolerant invaders, but new benign environment favors exotic over native	As environmental stress increases, invasion reduced (Gerhardt and Collinge 2003, Collinge et al. 2011).	Individualistic community succession (Gleason 1926) Environmental heterogeneity allows coexistence and reduces invader impact (Melbourne et al. 2007)
Fluctuating resource availability (Davis et al. 2000)	Invasion outcome is largely determined by given resource availability at a location	Supportive evidence from a field experiment manipulating resource availability (Davis and Pelsor 2001)	Resource availability=amount of unused resource = net balance between resource supply and uptake
Altered disturbance regimes (Hobbs and Huenneke 1992)	Any events to alter historical disturbance regime will increase risk of invasion	Disturbances enrich N and remove competitor, promoting <i>P. australis</i> (Minchinton and Bertness 2003)	Inhibition model in succession theory (Connell and Slatyer 1977)
<u>Propagule pressure</u>			
Propagule pressure (Lockwood et al. 2005, Simberloff 2009)	Invasion outcome is largely determined by propagule pressure	Propagule pressure overwhelms ecological resistance (Holle and Simberloff 2005)	

Table 2-2: Relationship between invaders' characteristics and invasiveness

Plant characteristics	Relationship	References
Transport		
Introduction year	-	(Bucharova and Van Kleunen 2009, Pyšek et al. 2009, Lavoie et al. 2013)
Human uses (introduction motive, nurseries, commercial availability, or dispersal via human body)	+	(Pyšek et al. 1995, Hodkinson and Thompson 1997, Lockwood et al. 2005, Van Kleunen et al. 2007, Lambdon et al. 2008, Hulme 2009, Chrobock et al. 2011)
Establishment/Colonization		
Specific leaf area§	+	(Lake and Leishman 2004, Hamilton et al. 2005, Van Kleunen et al. 2010)
Leaf size	+	(Williamson and Fitter 1996, Hamilton et al. 2005, Lloret et al. 2005, Van Kleunen et al. 2010)
CSR plant strategies§	CR+, C+, R+	(Pyšek et al. 1995, Prinzing et al. 2002, Pyšek et al. 2009)
Seedling vigor	+	(Pyšek and Richardson 2007, Van Kleunen and Johnson 2007b)
Growth rate§	+	(Frappier and Eckert 2003, Pyšek and Richardson 2007, Van Kleunen et al. 2010, Dawson et al. 2011)
Plant life span§	-	(Franco and Silvertown 1996, Hamilton et al. 2005)
Plant height§	+	(Gaudet and Keddy 1988, Funk et al. 2008)
Leaf nitrogen content§	+	(Funk et al. 2008)
Leaf mass per area (= 1/leaf dry matter contents§)	+	(Funk et al. 2008)
	-	
Abundance		
Native range	+	(Broennimann and Guisan 2008, Pyšek et al. 2009, Schlaepfer et al. 2010, Lavoie et al. 2013)
Study region	+	(Broennimann and Guisan 2008)
States in North America	+	(Broennimann and Guisan 2008)
Dispersal		
Seeds per shoot	+	(Cadotte and Lovett-Doust 2001, Van Kleunen and Johnson 2007b, Pyšek et al. 2009, Van Kleunen et al. 2010)
Seed mass§	-	(Cadotte and Lovett-Doust 2001, Lake and Leishman 2004, Hamilton et al. 2005)

Seed releasing height	+	(Nathan et al. 2002)
Terminal velocity	-	(Nathan et al. 2002)
Dispersal vectors	+	(Higgins et al. 2003, Lake and Leishman 2004, Llor et al. 2005)
Seed spread rate	+	(Belzile et al. 2010)
Vegetative reproduction	+	(Cadotte and Lovett-Doust 2001, Lloret et al. 2005, Song et al. 2013)
Vegetative spread rate	+	(Lake and Leishman 2004, Lloret et al. 2005)
Age of first flowering	-	(van Kleunen et al. 2011)
Flowering period	+	(Goodwin et al. 1999, Lake and Leishman 2004, Hamilton et al. 2005, Pyšek et al. 2009, Van Kleunen et al. 2010, Wolkovich and Cleland 2010)
Persistence		
Manageability	-	(Kettenring and Adams 2011)
Seed longevity	+	(Pyšek and Richardson 2007, Van Kleunen et al. 2010)
Buds below ground	+	(Van Kleunen et al. 2010)
Re-sprout ability	+	(Frappier and Eckert 2003, Van Kleunen et al. 2010)
Impact		
Negative impacts on ecosystem, agriculture, economy	+	(Direct indicatives)

[§]Functional traits that are used to categorize wetland plants into functional groups

Table 2-3: Research projects applying plant restoration to control invasion

Invasive plants	Research projects; ecosystem/context	Treatments; research questions	Main results
<i>Phragmites australis</i> (common reed)	Field experiment in salt marsh (Peter and Burdick 2010)	Transplanting of shoots of <i>P. australis</i> with plots with four native halophytes (~1,200 shoots m ⁻²)	Inhibited 60% of root-mediated invasion there is diversity effect <i>Spartina alterniflora</i> was most resistant
	Field experiment in salt marsh (Wang et al. 2006a)	Clearing <i>P. australis</i> and planting tissue culture regenerating of native plants	<i>Spartina patens</i> established dense stems in a salt marsh
	Field observation along highway (Albert et al. 2013)	Observe the relationship between tree cover and <i>P. australis</i> present/absent	Tree cover well explains presence and absence of the invader.
<i>Phalaris arundinacea</i> (reed canarygrass)	Wetland mesocosm experiment (Reinhardt Adams and Galatowitsch 2008)	Sowing density of the invader (0, 10, 50, 100, or 500 seeds m ⁻²) and a mix of native species (3000 or 15000 seeds m ⁻²)	High quantity of native seeds suppressed invader biomass, but did not block its invasion completely.
	Wetland mesocosm (Lindig-Cisneros and Zedler 2002c)	Applying seed mixtures in combination of six native species and a matrix of <i>Glyceria striata</i>	High canopy complexity hindered <i>P. arundinacea</i> 's growth
	Field experiment in wetland (Iannone III and Galatowitsch 2008)	Applying sawdust (high C:N ratio) to lower available nitrogen in soil	Treatment delayed establishment and decreased invader by 59%
<i>Centaurea diffusa</i> (knapweeds)	Field experiment in grassland (Meiman et al. 2009)	Native grass stem density (interspace between plant stems: 0, 5, and 15-cm)	More emergence in 0 cm than in 5 and 15-cm opening. Four individuals emerged out of 3,600 seeds input in control plot (8 m ⁻²)
<i>Rapistrum rugosum</i> (annual bastard cabbage)	Field experiment (Simmons 2005).	Sowing native Indian blanket (<i>Gaillardia pulchella</i>) at different sowing	The highest sowing density (10g m ⁻²) reduces 83% of invasion from seeds and

		densities	72% of aboveground biomass.
<i>Persicaria perfoliata</i> (annual Mile-a-minute weed)	Field experiment (Cutting and Hough-Goldstein 2013)	Sowing native seeds and biocontrol weevils (<i>Rhinoncomimus latipes</i>)	reduce 75% of invasion synergetic effects by combining the natural enemy of the plant and competitors
<i>Cardaria draba</i> , <i>Cirsium arvense</i> , <i>Bromus tectorum</i> , and <i>Bromus japonicas</i>	Greenhouse experiment (Perry et al. 2009)	Sowing seeds of annual cover crops	some of annual cover crops (Ragweed and Sunflower) control less than 50% of invasion of <i>Cirsium arvense</i> , and <i>Cardaria draba</i> , but facilitate invasion by other species (<i>Bromus tectorum</i> , <i>Bromus japonicas</i>)
<i>Arundo donax</i> (a gaint weed)	Field experiment of riparian restoration (Quinn and Holt 2009)	Community compositions including two densities of monoculture and all possible mixtures of a sedge, a shrub, and a tree species	The invasion was the least in a mixture of a shrub and a tree; The effects in the first year do not continue in the second year.

2.7. Figures

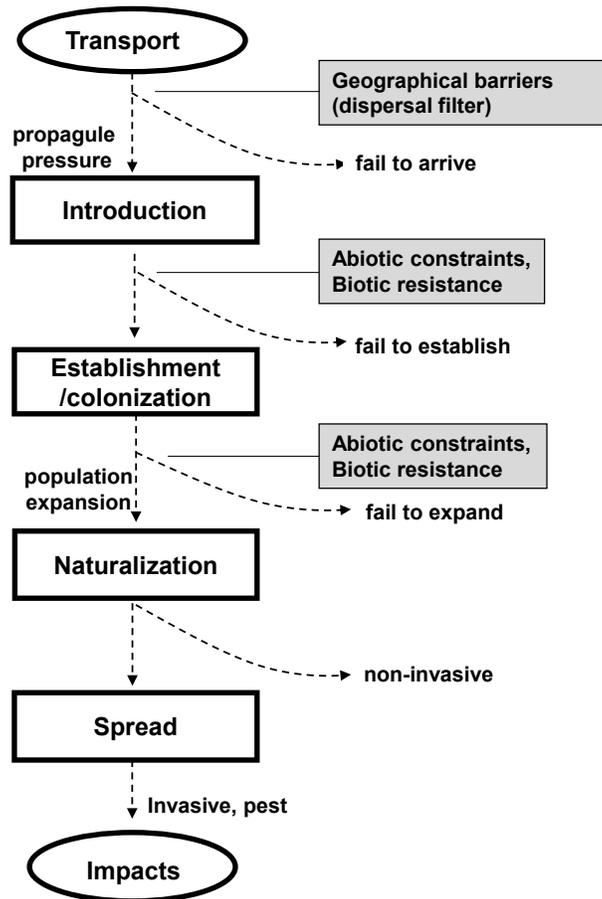


Figure 2-1: The biological invasion process and major determinants of propagule pressure, abiotic constraints and biotic resistance

Modified from previous models (Kolar and Lodge 2001, Catford et al. 2009)

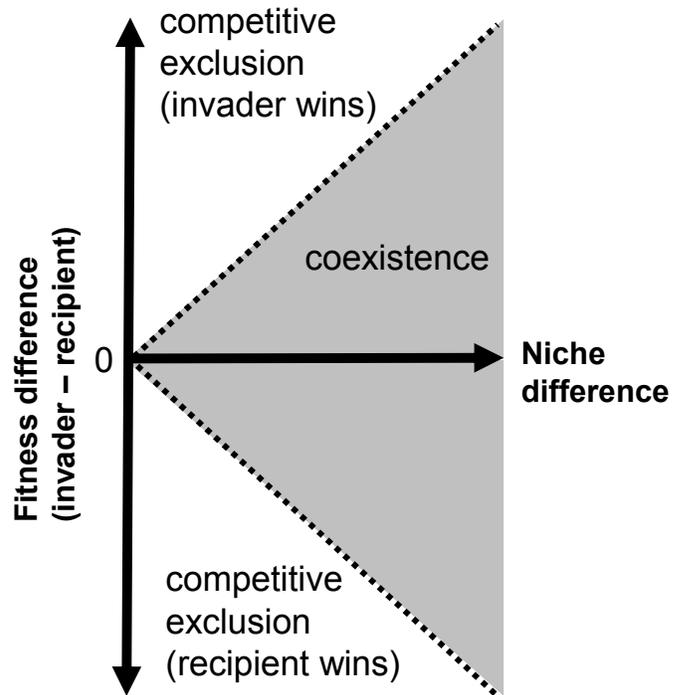


Figure 2-2: Roles of niche and fitness difference in determining outcome of invasion

(invader wins, or recipient wins, or coexistence)

Modified from MacDougall et al. (2009)

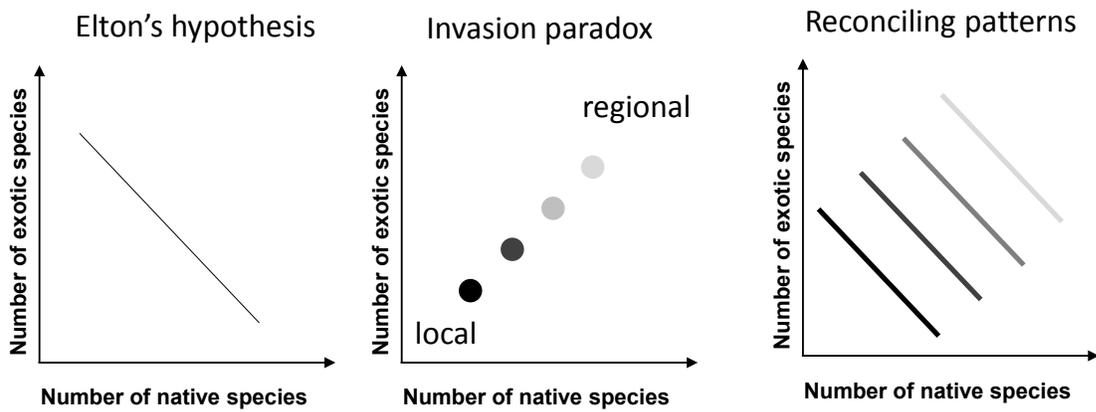


Figure 2-3: Elton's diversity-resistance hypothesis, Invasion paradox, and reconciled patterns (Levine and D'Antonio 1999, Fridley et al. 2007).

Modified from Shea and Chesson (2002). The shades of gray represent different scales.

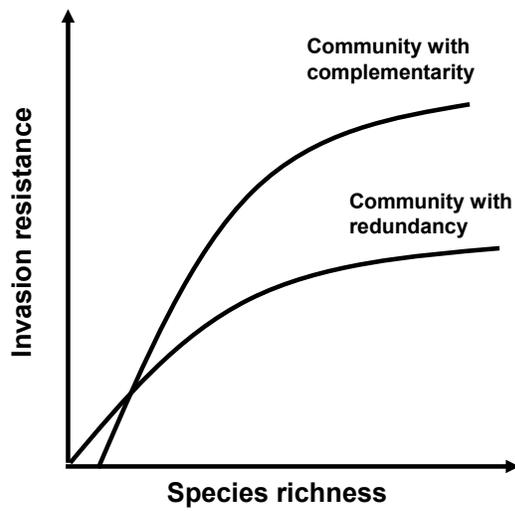


Figure 2-4: Role of functional diversity (community-wise complementarity) in biotic resistance, modified from Funk et al. (2008).

Diverse communities partitioning niches and to use resources most effectively. In addition, complementarity among species promotes a trade-off: functionality enhances additional diversity effects.

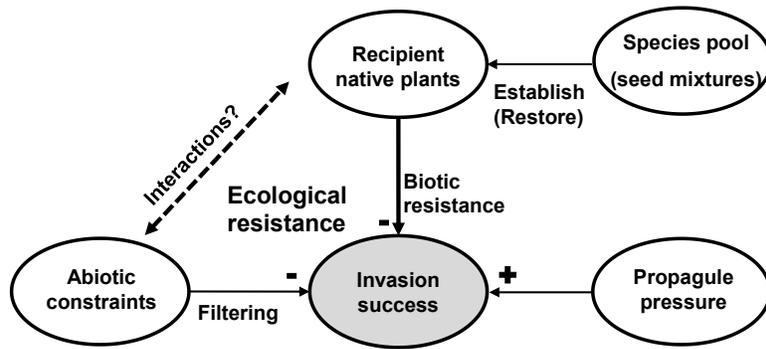


Figure 2-5: Systematic interplay among factors involved in biological invasion.

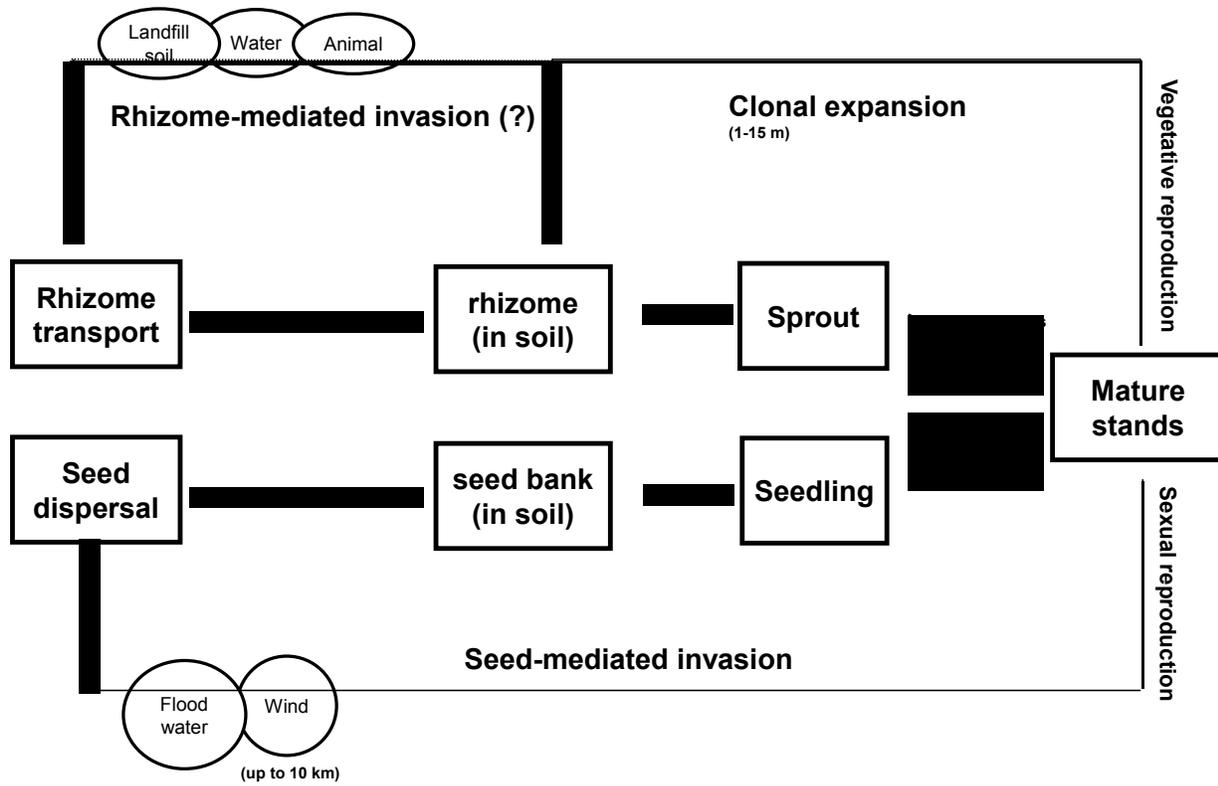


Figure 2-6: Invasion pathway of *Phragmites australis*

Chapter 3 Plant functional group identity and diversity determine biotic
resistance to invasion by an exotic grass

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3.1. Abstract

Biotic resistance, the ability of species in a community to limit invasion, is central to our understanding of how communities at risk of invasion assemble after disturbances, but it has yet to translate into guiding principles for the restoration of invasion-resistant plant communities. We combined experimental, functional, and modelling approaches to investigate processes of community assembly contributing to biotic resistance to *Phragmites australis*, a model invasive species in North America.

We hypothesized that (1) functional group identity would be a good predictor of biotic resistance to *P. australis*, while species identity effect would be redundant within functional group, and (2) mixtures of species would be more invasion-resistant than monocultures. We classified 36 resident wetland plants into four functional groups based on eight functional traits. We conducted two competition experiments based on additive competition design with *P. australis* and monocultures or mixtures of wetland plants. As an indicator of biotic resistance, we calculated a relative competition index (RCI_{avg}) based on the average performance of *P. australis* in competition treatment compared to control. To explain diversity effect further, we partitioned it into selection effect and complementarity effect and tested several diversity-interaction models.

In monoculture treatments, RCI_{avg} of wetland plants was significantly different among functional groups, but not within each functional group. We found the highest RCI_{avg} for fast-growing annuals, suggesting priority effect. RCI_{avg} of wetland plants was significantly greater in mixture than in monoculture mainly due to complementarity diversity effect among functional groups. In diversity-interaction models, species interaction patterns in mixtures were described best by interactions between functional groups when fitted to RCI_{avg} or biomass, implying niche partitioning.

Synthesis. Functional group identity and diversity of resident plant communities are good indicators of biotic resistance to invasion by introduced *P. australis*, suggesting niche pre-emption (priority effect) and niche partitioning (diversity effect) as underlying mechanisms. Guiding principles to understand and/or manage biological invasion could emerge from advances in community theory and the use of a functional framework. Targeting widely distributed invasive plants in different contexts and scaling up to field situations will facilitate generalization.

Key-words: Community assembly, diversity and invasibility, diversity-interaction model, ecological restoration, niche partitioning, invasive plant management, limiting similarity, *Phragmites australis*, priority effect, wetland invasion

3.2. Introduction

Biotic resistance refers to the ability of species in a community to limit the recruitment or invasion of other species from the regional pool (Levine et al. 2004, Catford et al. 2009). Biotic resistance has a long history in community ecology (Elton 1958, Fox 1987, Levine and D'Antonio 1999, Prieur-Richard et al. 2000, Pokorny et al. 2005, Fridley et al. 2007) and has been well documented, particularly against invasive plants (Davis et al. 2000, Lindig-Cisneros and Zedler 2002c, de Blois et al. 2004, Simmons 2005, Iannone III and Galatowitsch 2008, Reinhardt Adams and Galatowitsch 2008, Meiman et al. 2009, Perry et al. 2009). It is central to our understanding of how communities at risk of invasion assemble after disturbances, but it has yet to translate into wide-ranging guiding principles for the ecological restoration of invasion-resistant plant communities (Zedler 2000, Bakker and Wilson 2004, Iannone III and Galatowitsch 2008, Hobbs and Richardson 2010a, Middleton et al. 2010). Identifying species interactions and processes of community assembly that contribute to biotic resistance (Levine et al. 2004, MacDougall et al. 2009) is a promising approach particularly with the most widely distributed invasive plants. The latter provide good models for comparing invasion patterns across communities and regions, allowing generalizations to emerge.

Several concepts from community ecology theory such as limiting similarity, fitness inequality, and the diversity-resistance hypothesis have been proposed to explain biotic

resistance (Shea and Chesson 2002, Funk et al. 2008, MacDougall et al. 2009). These are not necessarily mutually exclusive as several processes may work synergistically or in alternation depending on context. Limiting similarity from classical competition theory (MacArthur and Levins 1967, Weltzin et al. 2003) postulates that a resident species whose niche overlaps with that of an invading species will compete most with the invader. When this happens, fitness inequality between resident species and the invader determines which species will be competitively excluded (MacDougall et al. 2009).

The diversity-resistance hypothesis predicts a positive relationship between species diversity and biotic resistance (Elton 1958). Small-scale experimental studies generally support Elton's hypothesis (Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Dukes 2002, Kennedy et al. 2002, Rinella et al. 2007, Frankow-Lindberg et al. 2009a, Frankow-Lindberg 2012) and so do competition-based models (Case 1990). It is assumed that diverse communities with broad niche breadth offer fewer niches for invaders. The so-called 'empty niche' concept remains controversial however, because non-invaded resident communities can have unsaturated niches (Tilman 1997). On the other hand, large-scale observational studies report opposite patterns (Stohlgren et al. 1999, Stohlgren et al. 2003). The scale dependence of the diversity-resistance relationship is further confirmed by observational studies that directly investigate the

effect of scales (Levine 2000, Brown and Peet 2003) and statistical models that consider both competition and resource available across communities (Byers and Noonburg 2003) or assumed null species interaction (Fridley et al. 2004). In other words, species-rich communities are more resistant to invasion than species-poor communities, meanwhile species-rich ecosystems and regions are likely to be hotspots not only for native species but also for exotic species (Fridley et al. 2007). The latter species may even be better adapted to their environment than the former (Shea and Chesson 2002, Callaway and Maron 2006, Verhoeven et al. 2009).

From a functional perspective, species-rich communities often result in high functional diversity when species show different functional traits and thereby strategies to acquire resources. Functional traits are defined as morpho-physio-phenological traits of species (Cornelissen 2003, Violle et al. 2007). Functional trait similarity between resident species and invading species is expected to lead to overlapping resource requirement and therefore competition (Funk et al. 2008). When species are grouped on the basis of similarity in functional traits, it is hypothesized that the lack of a certain functional group in a resident community will make that community more susceptible to invasion by a species from that functional group (Fox 1987, Von Holle and Simberloff 2004).

Functional group identity and diversity in resident community should therefore be good predictors of biotic resistance.

Several studies have used pre-defined functional groups such as growth form to test limiting similarity (Tilman 1997, Prieur-Richard et al. 2000, Symstad 2000, Booth et al. 2003, Von Holle and Simberloff 2004, Pokorny et al. 2005, Sheley and James 2010), but these groups often ignore functional traits that may be relevant to biotic resistance. For instance, functional traits such as specific leaf area, height at maturity, and seed mass in Westoby (1998)'s LHS plant ecology strategy were shown to correlate with plant invasiveness (Hamilton et al. 2005). Moreover, some invasive species take advantage of temporal niches when these are not occupied by other species (Wolkovich and Cleland 2010, Wilsey et al. 2011) so functional traits related to life history strategies, such as life longevity, determine the timing of species establishment and possibly competitive outcomes. Species that establish early and grow fast may lead to priority effect by pre-empting resources, leading to inhibition of the slow-growing species in community assembly (Mwangi et al. 2007). It is therefore important to classify species into functional groups based on several relevant traits to relate functional group identity with biotic resistance.

The diversity effect on biotic resistance can be further partitioned into selection effect and complementarity effect (Loreau 1998, Loreau and Hector 2001). Selection effect refers to the situation where the dominance of species with particular traits will

determine the diversity effect, whereas complementarity effect describes a situation where resource partitioning among species or positive species interactions contributes most to the diversity effect. Loreau and Hector (2001) proposed an additive partitioning diversity effect equation to help separate complementarity effect from selection effect, thereby allowing the assessment of their respective contribution to biotic resistance. Furthermore, by comparing different models based on different ecological assumptions about species interactions, diversity-interaction models (Kirwan et al. 2009) permit predictions of the relationship between diversity and function such as biotic resistance across different community composition. Partitioning diversity effect as well as applying diversity-interaction models promise new insights in relation to invasion resistance (Frankow-Lindberg et al. 2009a, Frankow-Lindberg 2012), especially if combined with a functional group approach.

We combined experimental, functional, and modelling approaches to investigate biotic resistance to *Phragmites australis*, a model species for large-statured invasive grasses in North America (Lambert et al. 2010). Genotype identity of species can influence their invasiveness (Vellend et al. 2010, Drummond and Vellend 2012) and currently three distinct lineages of *P. australis* are recognized in North America, including one of Eurasian origin (principally haplotype M, Saltonstall 2002), which is widely distributed and invasive in many regions. Given its cosmopolitan distribution, the characterization

of the genetic diversity of *P. australis* is an active area of research (Saltonstall 2002, Meyerson et al. 2010, Hauber et al. 2011, Lambertini et al. 2012, Meyerson et al. in press). Recent evidence shows that seed dispersal is the main strategy to colonize new sites (Alvarez et al. 2005, Fér and Hroudová 2009, Belzile et al. 2010), with roadside or ditches offering well connected habitats (Maheu-Giroux and de Blois 2007, Jodoin et al. 2008, Brisson et al. 2010). A niche opportunity is provided for seed germination and seedling establishment of *P. australis* when disturbance removes the vegetation cover and exposes bare soil (Minchinton and Bertness 2003). *P. australis* is being controlled largely through the abundant use of chemicals with little consideration for fundamental ecological principles or knowledge of species interactions. In areas where biodiversity is considered valuable or where *P. australis* is a major nuisance, for instance within or near protected reserves, restoring invasion-resistant wetland plant communities along potential invasion foci could be an innovative management strategy to constrain *P. australis*' expansion (Wang et al. 2006a, Carlson et al. 2009). Even in situations where control is not an option, it is fundamental to understand how communities at risk of invasion assemble after disturbances. Few studies have tested the relevance of biotic resistance to the restoration of wetland communities (Wang et al. 2006a, Carlson et al. 2009, Peter and Burdick 2010).

We investigated relative competitive effect of resident species (our measure of biotic resistance) on seedling establishment of *P. australis* using pot experiments simulating community assembly. Based on the assumption that some species, or combination of species, would be more resistant to invasion than others, we hypothesized that (1) functional group identity would be a good predictor of biotic resistance to *P. australis*, while species identity effect would be redundant within functional group, and (2) mixtures of species would be more invasion-resistant than monocultures due to either selection effect or complementarity diversity effect. This study allowed us to identify and evaluate species interaction processes such as niche overlapping, niche pre-emption, and niche partitioning contributing to biotic resistance to invasion.

3.3. Materials and methods

Overview of Experimental Design

We classified wetland plants, considered the resident species in our design, into four functional groups based on eight functional traits (life longevity, seed dry mass, specific leaf area, leaf nitrogen content, relative growth rate, growth form, leaf dry matter content, and height at maturity). We conducted two experiments based on additive competition design (Connolly et al. 2001) to evaluate the biotic resistance of wetland plant(s) to invasion by *P. australis* seedlings. In the first experiment starting in 2009, 11 wetland plants from three functional groups were tested in either monoculture (one

species + *P. australis*) or species mixtures (3 or 4 species + *P. australis*) with controls (only *P. australis*). In 2011, the second experiment tested 25 wetland plants, eight of which also tested in the first experiment, from four functional groups in monoculture with *P. australis*. In both experiments, biotic resistance of wetland plants was estimated by a relative competition index measuring how much *P. australis*' establishment and growth was reduced in competition treatments compared to control (without competition). The monoculture treatments allowed us to test the hypothesis about functional group effect versus species identity effect within each functional group. The mixture treatments of the first experiment allowed us to test diversity effect by comparing biotic resistance in monoculture versus mixture and investigating species interaction patterns that contribute to biotic resistance. To explain further this diversity effect, we partitioned diversity effect into selection effect and complementarity effect and we built diversity-interaction models describing biotic resistance as a function of different levels of species interactions.

Species Selection and Functional Classification

We chose 36 wetland herbaceous plants that are found at least 50% of the time in freshwater wetlands (OBL, FACW, or FAC in wetland indicator status in United States Department of Agriculture's PLANTS database). These plants represent a selection among the regional species pool, constrained by seed availability. Random subsets of

these species were used for the experiments reported in this study and for a related field experiment (Chapter 5). All species tested are native except *Lolium multiflorum* that is introduced but naturalized in the study region (Lavoie et al. 2012). Species nomenclature and status (native or introduced) in this study follow the Flora of North America (Flora of North America Editorial 1993) and the database of Vascular Plants of Canada (VASCAN), respectively.

We classified the wetland plants into emergent functional groups based on the following functional traits: life longevity, seed dry mass, specific leaf area, leaf nitrogen content, relative growth rate, growth form, leaf dry matter content, and height at maturity. These functional traits are relevant to leaf-height-seed plant ecology strategy scheme (Westoby 1998), the common core list of plant traits related with dispersal, establishment, and persistence (Weiher et al. 1999), functional traits related with competitive ability and growth (Funk et al. 2008), and functional classification of wetland plants (Boutin and Keddy 1993). Most numerical functional trait information was obtained from TRY global database of plant traits (Kattge et al. 2011b). We used the median value of several measurements of functional trait per each species from the TRY database for data consistency. For life longevity, we allocated annual for therophytes in Raunkiær life form and perennial for the others referring to Flora of Canada (Scoggan 1978). For growth form, we referred to the United States Department

of Agriculture's PLANTS database (<http://plants.usda.gov>) and followed their definition (single crown, single stem, bunch, stoloniferous, and rhizomatous). Based on these functional traits, Gower's similarity coefficient among species was calculated using `gowdis` function in R (Gower 1971, Podani 1999). All traits were standardized and equally weighted in the calculation of the similarity coefficient. Average similarity coefficient to *P. australis* was 0.40 in FG 1, 0.58 in FG 2, 0.72 in FG 3, and 0.76 in FG 4, respectively (Appendix 3-1; see Appendices in the last pages of thesis). Similarity coefficient to *P. australis* was significantly different among FG 1, FG 2, and FG 3, but not between FG 3 and FG 4 (Contrast test; $F_{1,31} = 0.96$, $P = 0.332$).

The 36 wetland plants were classified into functional groups using cluster analysis with ward option using `hclust` functions in R packages (Figure 3-1:). Classification led to the definition of four functional groups differing mostly by life longevity, growth form, height at maturity, and seed mass (Appendix 3-2). Species in functional group 1 (hereafter, FG 1) were annual plants characterized by the highest seed mass but the lowest height at maturity among species. Species in FG 2 were short perennial plants without rhizome characterized by the lowest seed mass. Species in FG 3 and FG4 were rhizomatous perennial plants. Species in FG 3 are short rhizomatous perennial plants, and species in FG 4 are tall rhizomatous perennial plants. *P. australis*, our target invader, belongs to FG 4.

Experiment Setting and Seed Preparation

We constructed outdoor pot experiments at the Montreal Botanical Garden to simulate a situation where seeds of *P. australis* arrive on bare soil after biological disturbance. Soil used in experiments was fertile clay soil, collected from a wetland basin in Saint-Etienne-de-Beauharnois, Quebec, Canada where *P. australis* is abundant. The soil was first sterilized using a steam pasteurizer at 76 °C for 4 hours to kill all viable seeds inside soil and thus prevent our system from contamination by unwanted species, while minimizing impact on natural soil physical properties. Soil was placed in each pot (diameter 10" and height 12"), and six pots were immersed in a large container, with water (see Appendix 3-3). Water level was maintained at -3 cm (\pm 1 cm) using an automatic water gauge device throughout the experiment.

Seeds of introduced *P. australis* (haplotype M) were collected in roadside ditches in Dundee in Quebec, Canada (N 45° 05', 50.6", W 74° 24', 36.4") in 2008. Most seeds of wetland plants were purchased from seed suppliers (© Prairie Moon Nursery; © Shooting Star Native Seeds) in North America at the time of the experiment. Seeds of each species were from single seed lot harvested from an identified ecotype in natural habitats across North America. The seeds of *Typha latifolia* and *Typha augustifolia* were collected from a pond at the Botanical Garden of Montreal for the second experiment.

Seed viability among wetland plants was standardized by applying the same number of pure live seeds per species to experimental units. Most pure live seed rate information was obtained from seed suppliers. Pure live seed rate is calculated by multiplying seed purity rate (excluding non-seed) and seed viability rate (excluding non-viable seeds) using standard tetrazolium testing procedures. All seeds, including *P. australis* ones, were cold-stratified at 3°C prior to the germination test, following standard methods (Lindig-Cisneros and Zedler 2001). Prior to the experiment, 50 seeds per species were placed in each of three Petri dishes with filter papers (Whatman® No. 1), moistened with 3 ml of distilled water, and sealed with Parafilm under fluorescent light (© GE; Plant & Aquarium T12®). We excluded any species with germination rate below 5 %. Pure live seeds per species, not seedlings, were applied for the pot experiments.

Competition Design

Additive competition design (Snaydon 1991, Keddy et al. 1994, Connolly et al. 2001) was used to test the competitive effect of resident species on *P. australis*. In the first experiment, 11 wetland plants were selected among three functional groups (FG 1, FG 2, and FG 3). They represent more than 25% of the species pool size of each FG. FG 4 had to be excluded in the first experiment as the seeds of species selected in this group such as *Typha augustifolia* did not germinate well enough in pre-germination test (less than 5%). Because trait similarity to *P. australis* were not significantly different between

FG 3 and FG 4 (Appendix 3-1), we conducted the first experiment without FG 4, assuming that biotic resistance to invasion by *P. australis* of FG 3 would be similar to that of FG 4 if trait similarity determines biotic resistance. We were, however, able to test this group in the second experiment with new seed lots. For mixture treatments, three or four species among the 11 species were randomly assigned to a mixture for a total of eight mixtures that represent a variety of functional group composition. There were 11 monocultures and 8 mixture treatments plus one control with *P. australis*; a total of 20 experimental units (treatment + control) were replicated three times in a randomized complete block design (RCBD).

All species in monocultures or mixtures were sown at the start of the growing season in 2009 along with seeds of *P. australis* in treatment or control. The seeding density of wetland plant(s) and *P. australis* were 210 and 70 pure live seeds per each pot respectively. We applied the 3:1 ratio of wetland plant to *P. australis* in seeding density to maximize the chances of detecting quantitative differences in biotic resistance among treatments. The total 280 pure live seeds of all species per each pot (surface area = 700 cm²) is equivalent to 4,000 seeds /m². This seeding density is within the range of the level (from 3,000 to 7,000 seeds /m²) found in soil seedbank of some restored wetlands and natural wetlands (Galatowitsch and van der Valk 1996). To verify whether biotic resistance changes with time, we took measurements in the monocultures at the end of the growing season in 2009 and again in 2010. Only monocultures were followed up for

two years. While pot experiments can provide an adequate setting for the first year of growth, they were not ideally suited for long-term monitoring of more complex species mixtures. Seeds were not reintroduced in pots for the second year of the monoculture experiment.

In addition, we conducted a second experiment with 25 wetland plants in 2011 to validate some of the findings of the first monoculture experiment. We used the same experimental design for monocultures as before but followed the experiment for the first growing season only and included a new functional group (FG 4). For seeding density, we kept the same level for *P. australis* (70 pure live seeds/ pot), but doubled the number of seeds of resident species (420 pure live seeds/ pot) based on the results of the first experiment to be able to compare biotic resistance more clearly among functional groups. It must be noted that we were aiming for experimental conditions that would lead to a quantitative response in terms of biotic resistance, not just a dichotomous one (invaded or not invaded).

Data Measurement and Analyses

At the end of the growing season, we measured the number of shoots, aboveground biomass, plant height, and plant cover of *P. australis* in each treatment and control pot to calculate the main response variable (see below). In addition, we also measured

plant cover, plant height, and aboveground biomass of all wetland plants to correlate them with the response variables. Plant cover was measured using point intercept method with a 40-cells mesh. For aboveground biomass, aboveground portion of plant were collected at the end of September of each year and stored in stove at 70 °C for 48 hours until weighed. Plant canopy height was estimated for each species to the closest 0.5 cm. We calculated the relative competition index (RCI) to estimate the competitive effect of wetland plant(s) on *P. australis* using the following equation (Weigelt and Jolliffe 2003):

$$RCI_Y = \frac{Y_{control} - Y_{treatment}}{Y_{control}} \quad \text{eqn 1}$$

Where, RCI is the relative competition index of wetland plant on *P. australis* in either monoculture or mixture for a given variable Y (number of shoots, aboveground biomass, plant height, or plant cover of *P. australis*). $Y_{control}$ is performance of *P. australis* in control, $Y_{treatment}$ is performance of *P. australis* in treatment. Because $RCI_{number\ of\ shoots}$, $RCI_{biomass}$, RCI_{height} , and $RCI_{plant\ cover}$ were highly correlated to each other (Appendix 3-4), we used RCI_{avg} , the arithmetic mean of $RCI_{number\ of\ shoots}$, $RCI_{biomass}$, RCI_{height} , and $RCI_{plant\ cover}$ as the main response variable for all analyses. A value of 0 for RCI_{avg} suggests no competitive effect on *P. australis*, a value of 1 suggests complete competitive exclusion of *P. australis*, and negative RCI suggests facilitation of *P. australis*' establishment and growth by wetland plants. Finally, we also calculated yearly

change of RCI_{avg} between 2009 and 2010 (ΔRCI_{avg}) to assess time effect on biotic resistance.

We used ANOVA to test for functional group identity effect and species identity effect nested within each functional group on RCI_{avg} or ΔRCI_{avg} for monoculture treatment in both experiments. The generalized linear mixed model (REML; F test) was used for this test to take into account random block effect (Bolker et al. 2009). Normality of residuals and homoscedasticity were checked and response variables were transformed when necessary. When significant functional group effect was found, we compared the mean of functional groups using contrast test on each pair of functional groups. If we found a significant species identity effect within each functional group, we used Tukey's HSD multiple comparison test to compare means of species identity effect by each functional group.

Partitioning Diversity Effect

The net diversity effect in mixture treatments of the first experiment was partitioned into selection effect and complementarity effect using the additive partitioning biodiversity effect equation (Loreau and Hector 2001). In the original equation, selection effect is calculated using a covariance function that relates yield of species in a mixture with one in monoculture, and the complementarity effect measures any change in the average

relative yield in the mixture. The net diversity effect (the sum of these two effects) represents the deviation of the yield in mixture from its expected yield value in monoculture and the relative abundance of species in the mixtures. Because the original equation was developed for yield, we replaced yield with RCI_{avg} , then we estimated the relative contribution of each species to RCI_{avg} in mixture based on the assumption that it is proportional to the relative plant cover of that species in the mixture (Appendix 3-5).

Diversity Interaction Model

As a complement to diversity equation, we used diversity-interaction models (Kirwan et al. 2009) to investigate species interaction patterns contributing to biotic resistance in the mixtures from the first experiment. Comparing models based on different ecological assumptions allows to test alternative hypotheses about the relative role of functional groups and functional redundancy in biotic resistance (Kirwan et al. 2009).

Model 1 describes species identity effect alone without species interaction:

$$y = \sum_{i=1}^s \beta_i P_i + \varepsilon \quad \text{eqn 2}$$

The response variable (y) represents RCI_{avg} as an indicator for biotic resistance to invasion by *P. australis*. β_i is the estimated performance of species i in contribution to biotic resistance, and P_i is the initial proportion of species i in seed mixture. In case of monoculture treatment of species i , P_i equal to 1.

Model 2 describes functional group identity effect alone without species interaction:

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \varepsilon \quad \text{eqn 3}$$

β_{FG1} is the estimated functional group identity effect of FG 1 and P_{FG1} is the sum of all species proportions within that FG 1.

Model 3 describes functional group identity effect and average species interaction:

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \delta_{av} \sum_{\substack{i,j=1 \\ i < j}}^s P_i P_j + \varepsilon \quad \text{eqn 4}$$

δ_{av} is the single interaction coefficient assuming that a pair of species interacts equally to contribute to such diversity effect.

Model 4 describes functional group identity effect and species interaction within and between functional group:

$$\begin{aligned} y = & \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} \\ & + \delta_{wFG1} \sum_{\substack{i,j=1 \\ i < j}}^t P_i P_j + \delta_{wFG2} \sum_{\substack{i,j=t+1 \\ i < j}}^{t+h} P_i P_j + \delta_{wFG3} \sum_{\substack{i,j=t+h+1 \\ i < j}}^s P_i P_j \\ & + \delta_{bFG1FG2} P_{FG1} P_{FG2} + \delta_{bFG1FG3} P_{FG1} P_{FG3} + \delta_{bFG2FG3} P_{FG2} P_{FG3} + \varepsilon \end{aligned} \quad \text{eqn 5}$$

Where δ_{wFG1} is the coefficient of pairwise species interaction within FG 1 and $\delta_{wFG1FG2}$ is the coefficient of pairwise species interactions between FG 1 and FG 2.

Model 5 describes functional group identity effect and separate pairwise species interactions:

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} P_i P_j + \varepsilon \quad \text{eqn 6}$$

Where δ_{ij} is the coefficient of separate pairwise interaction between species i and species j

Model 6 describes functional group identity effect and species interactions between functional group without species interaction within each functional group:

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \delta_{bFG1-FG2}P_{FG1}P_{FG2} + \delta_{bFG1-FG3}P_{FG1}P_{FG3} + \delta_{bFG2-FG3}P_{FG2}P_{FG3} + \varepsilon \quad \text{eqn 7}$$

Each model was tested using glm function in R software. Pairs of models were compared for significant difference in model predictions for RCI_{avg} using anova.lm function in R software. Using Model 6, we estimated model prediction about the effect of functional group composition (both functional group identity and interaction) on RCI_{avg} using predict function in stats package in R software. The model prediction on response surface was drawn in ternary plot using levelplot function in lattice package in R software.

All ANOVA tests and correlation analyses were conducted using the JMP software (© SAS Institute Inc.). Partitioning diversity effect was calculated using mathematical equations in the Excel software (© Microsoft). Cluster analysis and diversity-interaction modeling, which is based on multiple regressions, were conducted using R (<http://www.r-project.org>).

3.4. Results

Monoculture Treatments

In monoculture treatments and for both experiments, relative competitive effect of wetland plants on *P. australis* was mostly related to their functional group identity while species identity effect remained redundant within each functional group (Figure 3-2 and Figure 3-3). In the 2009 experiment, relative competitive index (RCI_{avg}) of 11 wetland plants on *P. australis* was significantly different among three FGs ($F_{2,20} = 46.62$, $P < 0.001$), but it was not significantly different within each FG ($F_{8,20} = 1.79$, $P = 0.137$). RCI_{avg} of FG 1 (annual plants) was the highest followed by FG 2 and FG 3 ($RCI_{avg} = 0.817$, 0.308 , and 0.166 respectively; Figure 3-2a). In 2010, we found a similar functional redundancy pattern. RCI_{avg} was significantly different among three FGs ($F_{2,20} = 47.43$, $P < 0.001$), but not within each FG ($F_{8,20} = 1.29$, $P = 0.299$). RCI_{avg} of FG 1 was the highest followed by FG 2 and FG 3 ($RCI_{avg} = 0.498$, 0.373 , and 0.131 respectively; Figure 3-2b). From 2009 to 2010, RCI_{avg} (hereafter, ΔRCI_{avg}) of FG 1 decreased but RCI_{avg} of FG 2 and FG 3 did not change greatly (Figure 3-2c). ΔRCI_{avg} was significantly different among three FGs ($F_{2,20} = 8.14$, $P = 0.002$), but not within each FG ($F_{8,20} = 0.30$, $P = 0.957$). RCI_{avg} of FG 1 decreased greatly ($\Delta RCI_{avg} = -0.319$), RCI_{avg} of FG 2 increased slightly ($\Delta RCI_{avg} = +0.064$), and RCI_{avg} of FG 3 decreased slightly ($\Delta RCI_{avg} = -0.035$; Figure 3-2c). When the same analysis was conducted replacing RCI_{avg} with biomass of *P. australis* for main response variable, similar functional redundancy pattern was found (Appendix 3-6).

Plant cover of wetland plants relative to *P. australis* also changed differently depending on functional group from 2009 to 2010 (Appendix 3-7). In 2009, FG 1 became dominant over *P. australis*, but *P. australis* became dominant over FG 2 and FG 3. In 2010, *P. australis* became dominant over FG 1 and FG 3, but FG 2 became dominant over *P. australis*. Wetland plants' performance traits were significantly correlated with RCI_{avg} in terms of biomass (Pearson coefficient, $r = 0.77$), height ($r = 0.61$), and plant cover ($r = 0.79$; Appendix 3-8). Among the plant functional traits used to classify functional group, relative growth rate ($r = 0.51$), seed mass ($r = 0.59$), and LDMC ($r = -0.36$), were significantly correlated with RCI_{avg} and annual plants with single crown or bunch in growth form showed relatively high RCI_{avg} (Appendix 3-8).

In the second experiment with 25 wetland plants including one additional FG (FG 4; tall perennial with rhizome), we found a functional redundancy pattern similar to the first experiment. In the second experiment, RCI_{avg} was arcsine-transformed to meet ANOVA's assumption about equal variance. RCI_{avg} was significantly different among four FGs (arcsine transformed; $F_{3,48} = 24.74$, $P < 0.001$), and RCI_{avg} was significantly different within one FG ($F_{21,48} = 1.78$, $P = 0.049$). RCI_{avg} of FG 1 was the highest, followed by FG 4, FG 2, and FG 3 ($RCI_{avg} = 0.877$, 0.687 , 0.540 , and 0.244 respectively; Figure 3-3). When the one-way ANOVA test was conducted on species identity effect alone within each functional group, there was no significant difference in RCI_{avg} among

species identity within FG 1 ($F_{3,6} = 3.71$, $P = 0.080$), FG 2 ($F_{6,12} = 0.68$, $P = 0.665$), and FG 3 ($F_{8,16} = 1.33$, $P = 0.294$), but there was one for FG 4 ($F_{4,8} = 10.28$, $P = 0.003$). The significant species identity effect within FG 4 was due to *Leersia oryzoides*, the most resistant species in this group.

Mixture Treatments

Mixtures of wetland plants were more resistant than monocultures, and such diversity effect on biotic resistance came from complementarity effect, from positive interactions between FG 1 and FG 3 in the first experiment (Figure 3-4 and Figure 3-5). RCI_{avg} was significantly greater in mixture than in monocultures ($F_{1,53} = 4.70$; $P < 0.034$; Figure 3-4a).

In partitioning diversity effect on RCI_{avg} in mixtures, complementarity effect rather than selection effect contributes most to the positive net diversity effect (Figure 3-4b).

Aboveground biomass of resident species was also significantly greater in mixture treatments than in monoculture treatments (Log-transformed; $F_{1,53} = 22.72$; $P < 0.001$) and partitioning diversity effect showed similar pattern (Appendix 3-9).

Comparison between a pair of diversity-interaction models fitted to the first experimental data revealed distinctive species interaction patterns by functional group contributing to biotic resistance. The functional group identity effect terms fitted as well as species identity effect terms (Model 1 vs 2; F test; $P = 0.157$). There was strong evidence of an

average interaction term effect (diversity effect) (Model 2 vs 3; F test; $P=0.001$). The species interaction by functional group (species interaction within and between functional group) terms fitted much better than single average interaction term (Model 3 vs 4, F test; $P<0.001$). However, the separate pairwise species interactions terms fitted no better than the species interaction by functional group term (Model 4 vs Model 5; F test; $P= 0.425$). There was no evidence of significant species interaction within each functional group (Model 4 vs Model 6, F test; $P= 0.269$). Thus, the last model (Model 6; functional group identity effect and species interaction between functional group) was chosen for the final model prediction because it fitted as well as complex models with separate pairwise species interactions.

Figure 3-5a shows Model 6 prediction about the effect of functional group composition in seed mixtures on biotic resistance to invasion by *P. australis*. Figure 3-5b shows the same model prediction when it was fitted to aboveground biomass instead of RCI_{avg} of wetland plants. In either case, we found a positive interaction between FG 1 and FG 3 in their contribution to biotic resistance. The highest RCI_{avg} and aboveground biomass were estimated when FG 1 and FG 3 were mixed in a ratio of 2 to 1, approximately. For further detail on model results and significant terms and their estimates, see Appendix 3-10.

3.5. Discussion

Functional group identity is a significant predictor of biotic resistance. The most consistent finding in our experiments is the strong contribution of annual plants (FG 1), even when different functional group combinations are tested. Combining functional groups in mixtures leads to complementarity effect resulting in higher biotic resistance than in monocultures. These findings suggest that processes such as niche pre-emption (selection effect of FG 1) and niche partitioning (complementarity diversity effect by functional group interaction) contribute to limit seedling establishment of *P. australis*.

Functional group and biotic resistance

Other studies relating biotic resistance to functional groups based on various plant traits such as life longevity, growth form, root structure, plant height, or photosynthetic pathway (Tilman 1997, Prieur-Richard et al. 2000, Symstad 2000, Dukes 2002, Bakker and Wilson 2004, Von Holle and Simberloff 2004, Pokorny et al. 2005, Lulow 2006, Mwangi et al. 2007, Sheley and James 2010) have found a significant effect of functional group on biotic resistance, with some exceptions (Von Holle and Simberloff 2004). Which functional group resists invasion better is not always consistent among studies though. In some cases, the functional group of resident species most similar to the invader offers the most resistance (Dukes 2002, Bakker and Wilson 2004, Pokorny et al. 2005, Mwangi et al. 2007), suggesting limiting similarity, whereas in other cases,

different functional groups resist better (Lulow 2006, Sheley and James 2010), suggesting fitness inequality as one of key resistance mechanism. MacDougall, Gilbert & Levine (2009) propose that invasion success may depend on both fitness advantage and niche difference from resident species. Recently, Kunstler et al. (2012) showed that competitive-ability related trait hierarchy rather than functional trait similarity (Funk et al. 2008) drives competitive interaction in community assembly. Contradictory patterns in community assembly, including for biological invasion, highlight the need for repeated measurements with a functional approach as we did.

It is unlikely that one functional group will dominate in all contexts and at all stages of community assembly, but given the conditions of our experiments, early and fast growing species (FG 1) were definitely the most resistant to invasion of *P. australis*, at least in the first critical year of community assembly. The fact that some annual plants grew faster than *P. australis* in the first experiment suggests priority effect by preempting niche to inhibit slower growing species in community assembly (Young 2001, Fukami et al. 2005, Mwangi et al. 2007). We found that *P. australis* is also capable of early and fast growth unlike many other perennial plants, and this could provide it with some competitive advantages over other groups such as FG 2 and FG 3. The ability to take advantage of a temporal niche early in the growing season also resulted in increased aboveground biomass and height of resident species, which are positively

correlated with biotic resistance (Appendix 3-8). Early emergence increases components of plant fitness such as seedling growth in a controlled experiment (Verdú and Traveset 2005). Biomass of resident communities has been documented as one of the best indicators for competitive ability (Gaudet and Keddy 1988) and level of biotic resistance (Lulow 2006). High biomass of resident species could imply less resource availability for invaders which lead to strong biotic resistance (Davis et al. 2000). On the other hand, legumes have been shown to facilitate invasion due to their ability to fix nitrogen (Mwangi et al. 2007, Frankow-Lindberg 2012). Most wetland plants that we tested, including *P. australis*, do not have nitrogen fixation ability in wetlands (Ehrenfeld 2003; TRY traits database).

Our results provide only partial evidence to support the role of limiting similarity in biotic resistance. Although the functional group which is most similar to *P. australis* (FG 4; tall perennial with rhizome) resists to invasion substantially, the order of functional group in level of biotic resistance (FG 1 \geq FG 4 \geq FG 2 > FG 3; Figure 3-2 and Figure 3-3) in the monoculture experiments was not consistent with the expected functional similarity with *P. australis* (FG 4 \geq FG 3 > FG 2 > FG 1; Figure 3-1.; Appendix 3-1). Interpretation from such direct comparison may be limited because functional traits of species are usually measured from mature plants and the importance of some traits will change with time

for a species (Cornelissen 2003, Kattge et al. 2011b). The effect of functional similarity therefore may increase with time as the community matures.

Our goal was to investigate the window of invasion opportunities during community reassembly after disturbances, a condition that often favours invasive plants through seedling establishment, but the second year of the monoculture experiments (in 2010) also provides some insights on how the biotic resistance of functional group may change with time. The annuals still offered the best resistance but that effect had begun to decrease. Considering general species turnover patterns between colonizers and competitors in plant succession (Tilman 1990), perennial plants may have benefit for biotic resistance as succession proceeds (Lockwood et al. 1997), but their effect at the time scale of our experiments was mostly through interactions. Longer term studies to test the effect of mixtures of functional groups on biotic resistance over time in field conditions are required to verify this assumption.

Diversity Effect on Biotic Resistance

Species mixtures are more resistant than monocultures and this result is consistent with previous community-scale experimental studies on multiple invaders (Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001, Dukes 2002, Kennedy et al. 2002, Frankow-Lindberg et al. 2009a) and specifically against *P. australis* (Peter and

Burdick 2010). Field observational studies reported similar pattern at community scale (Levine 2000, Brown and Peet 2003), but opposite pattern at larger scale (Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003, Stohlgren et al. 2003). Spatially covarying environmental factors such as resource availability or disturbance regime can affect both diversity and invasibility (Levine and D'Antonio 1999, Byers and Noonburg 2003, Davies et al. 2007a). Furthermore, different ecological processes such as dispersal and community recruitment can predominate at large scale (Tilman 1997, Pauchard and Shea 2006, Fridley et al. 2007).

More importantly, the complementarity-diversity effect in our study is best explained by positive species interactions between functional groups, implying niche partitioning among species mixtures. When selection effect is positive and strong, dominant species identity is expected to matter to invasion resistance (Emery and Gross 2007). In such case, fitness advantage of a species rather than niche complementarity among species determines biotic resistance of mixtures. The main selection effect observed in our study was a positive selection effect with FG 1 plants such as *Lolium multiflorum* and *Bidens sp.*, and negative selection effect in mixture with FG 3 plants such as *Eupatorium sp.* Interestingly, our study also shows that selection effect varies with functional group composition in mixtures. In other experiments, there was a strong selection effect of *Spartina alterniflora* on *P. australis* (Peter and Burdick 2010) or

Lolium perenne on multiple invaders (Frankow-Lindberg 2012). Both selection and complementary effect contributed to biotic resistance (Fargione and Tilman 2005) and the relative contribution of selection and complementarity effect may vary with the species and functional groups involved.

Our results in diversity-interaction models suggest species interactions between functional groups contribute to complementarity diversity effect by increasing biomass of resident communities (Figure 3-5). This result provides indirect evidence for resource partitioning between functional groups in our system. Functionally diverse resident communities can use resource more completely than simple community (Prieur-Richard et al. 2000, Pokorny et al. 2005, Davies et al. 2007b, Rinella et al. 2007). Other investigation of resource uses pattern such as soil nitrogen uptake have provided more direct evidence for resource partitioning of diverse community in relation to biotic resistance (Tilman 1997, Booth et al. 2003). Furthermore, functionally diverse communities with their complex canopy allow less light penetration through the canopy (Lindig-Cisneros and Zedler 2002c, Frankow-Lindberg 2012).

Implication for Management

In field situations, invasion success will be determined by the interplay between environmental conditions, propagule pressure, and biotic resistance (D'Antonio 1993,

Dethier and Hacker 2005, Perelman et al. 2007, Catford et al. 2009). Wetlands being nutrient sinks, excess nutrient supply coupled with disturbance to the vegetation cover will tend to increase vulnerability to invasion (Burke and Grime 1996, Huston 2004, Lake and Leishman 2004), especially since seedlings of introduced *P. australis* establish on bare fertile soil. Altered flood regimes, especially prolonged drawdown conditions, which may become common with climate change and increasing demand on water, will further facilitate seedling establishment of *P. australis* (Mauchamp et al. 2001). Such conditions would provide the optimal window of opportunity for *P. australis*, possibly serving as invasion foci. This highlights the need, where applicable, to minimize damage to the matrix vegetation cover and/or to facilitate the rapid establishment of a competitive cover if the goal is to restore disturbed habitats. In these cases, functional group identity and diversity of resident or restored plant communities will be good indicators of potential biotic resistance to seed-mediated invasion by introduced *P. australis*. As for propagule pressure, most field situations are expected to show much lower seed pressure than the one tested in our experiment, but even then, complete competitive exclusion may not be reached. Follow-up monitoring and selective control of *P. australis* establishment could be necessary.

Our study indicates that guiding ecological principles to understand and/or manage, if desirable, biological invasion could emerge from advances in community theory and the

use of a functional framework. Targeting widely distributed invasive plants in different contexts and scaling up to field situations will facilitate generalization. We are currently conducting such a large scale field experiment to test whether the ecological principles uncovered in this study apply to a more complex, realistic setting.

3.6. Figures

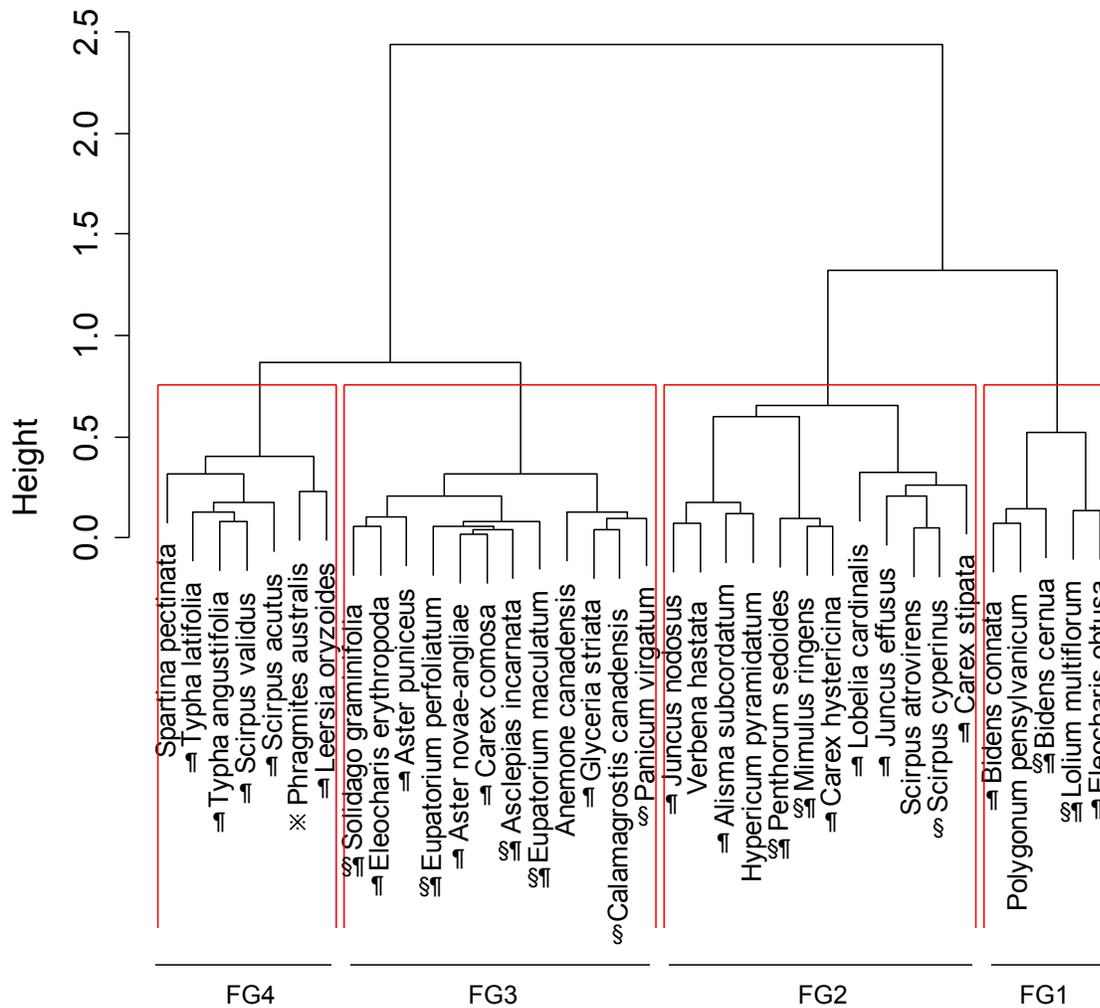


Figure 3-1: Classification of 36 wetland plants into four functional groups by functional trait similarity.

§Species selected for the first experiment, ¶Species selected for the second experiment

*Target invasive species in the experiments

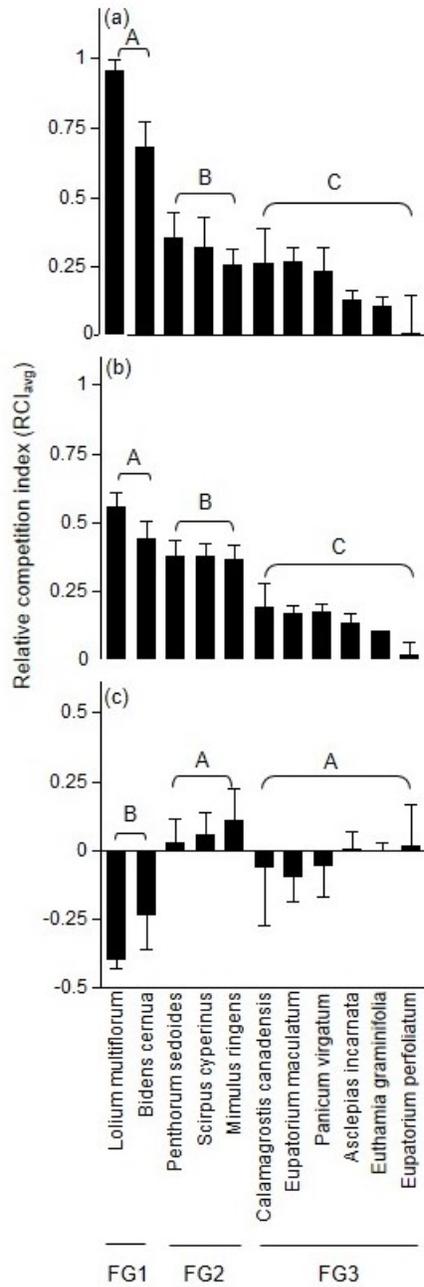


Figure 3-2: The relative competition index of monoculture (RCI_{avg}) of a wetland plant (a) in 2009, (b) in 2010, and (c) yearly change in the first experiment.

Error bar shows standard error of mean. Functional groups connected by same letter are not significantly different from each other.

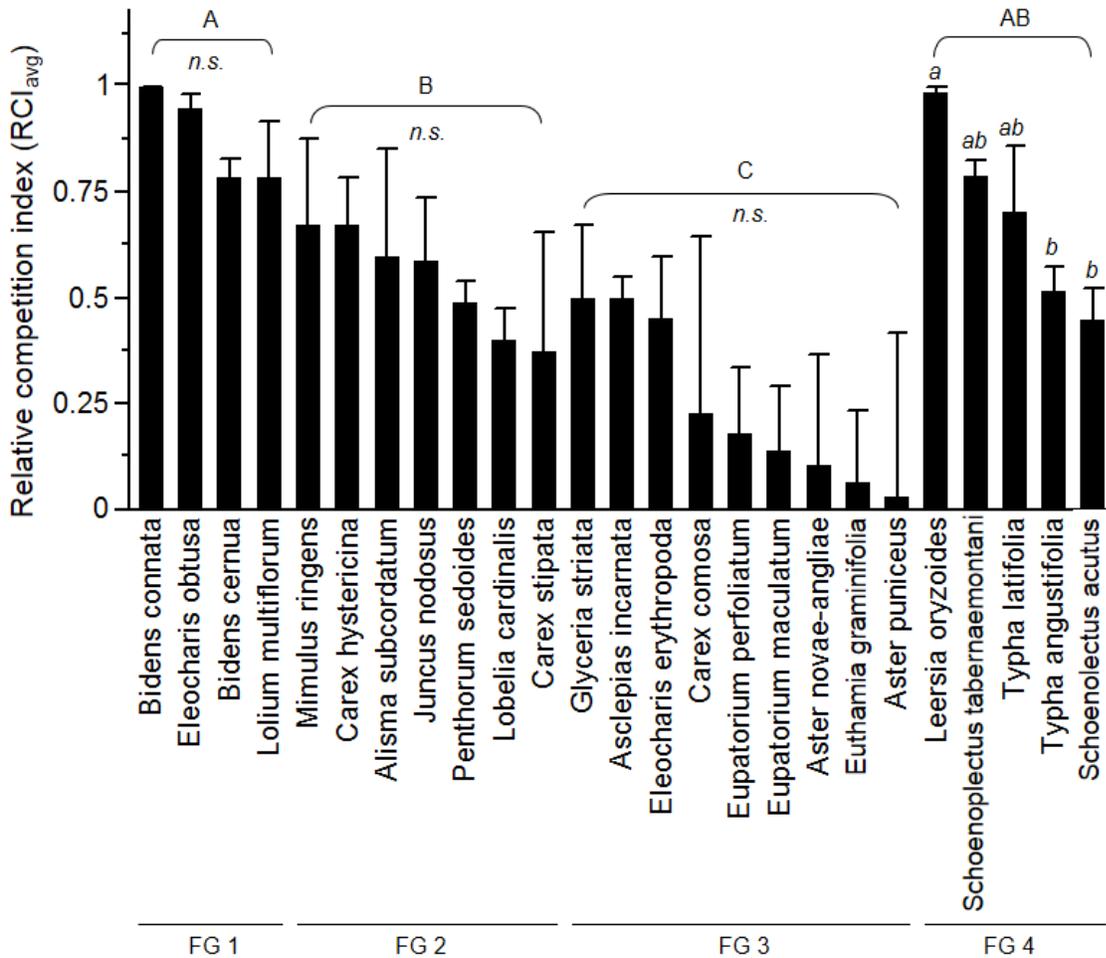


Figure 3-3: The relative competition index of monoculture (RCI_{avg}) of a wetland plant in the second experiment in 2011.

Error bar shows standard error of mean. Functional groups connected by same capital letters (A, B, C) are not significantly different from each other. Within each functional group, species connected by same lower-case letter (a or b) or “n.s.” are not significantly different.

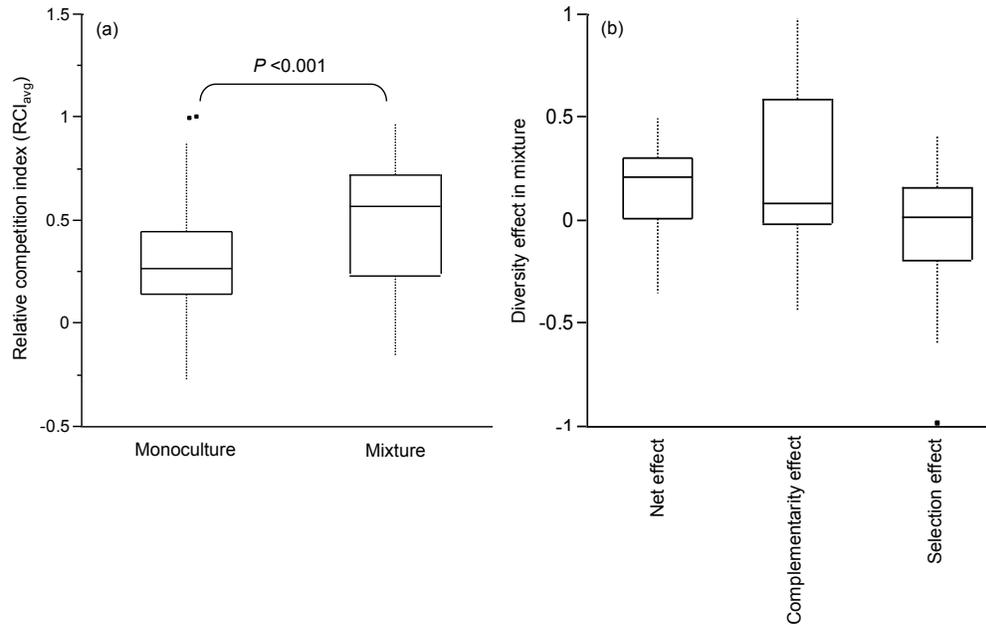


Figure 3-4: (a) Relative competition index of monoculture and mixture of wetland plants in the first experiment. (b) Partitioning diversity effect into selection effect and complementarity effect

Applying additive partitioning diversity effect equation (Loreau & Hector 2001).

P values represent contrast test to compare mean.

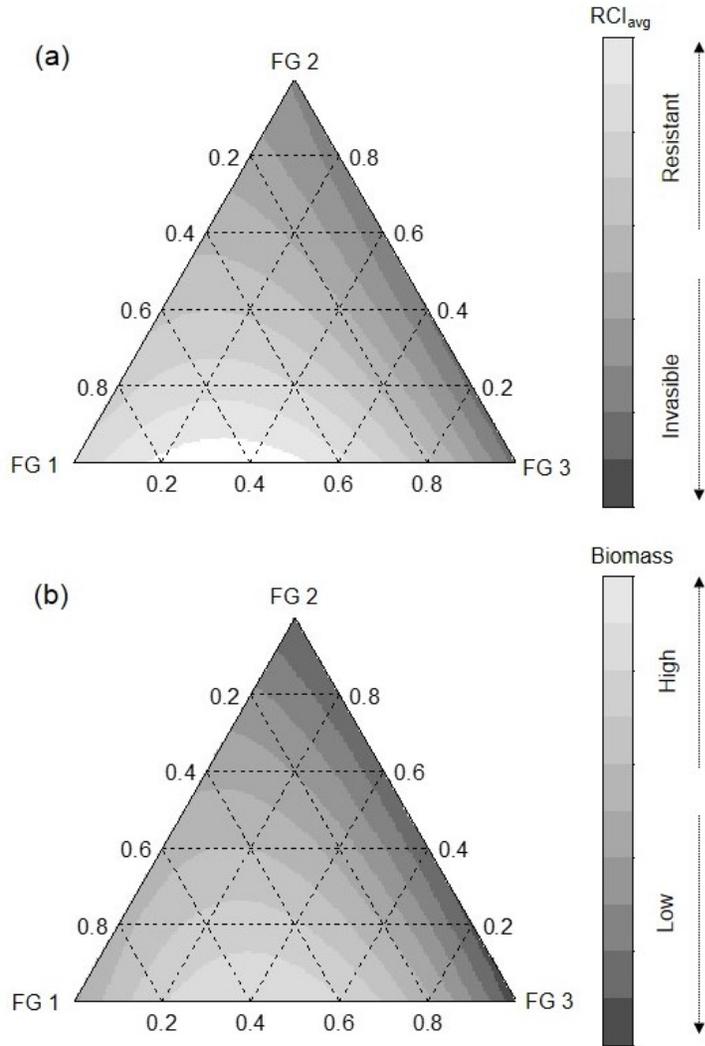


Figure 3-5: Biodiversity-interaction model prediction about the effect of functional group composition on (a) RCI_{avg} : relative competition index of wetland plant(s) as indicator of biotic resistance and (b) aboveground biomass of wetland plant(s) per pot (g), estimated from the first experiment data in 2009. Each corner of the ternary plot represents monoculture of each functional group, whereas inner area of the plot represents mixture of functional groups. For details about the model equation, see equation 7.3.7.

3.7. Connections to the next Chapter

In Chapter 3, I investigated plant functional traits-based resistance mechanisms in relation to the niche (Byun et al. 2013). I found the importance of functional characteristics (or functional group identity) of recipient species in determining biotic resistance of a community. Short fast growing annual plants (FG 1) are the most resistant functional group among 35 wetland plant species and this suggests that priority effect plays a significant role to resist *P. australis* invasion, but limiting similarity (i.e. a functional group, the same as *P. australis*) showed only marginal effect. In addition, mixture of four species is more resistant than monoculture of one species. Partitioning diversity effect and diversity-interaction suggest that niche partitioning generates diversity effect in biotic resistance; the study also contributes to fundamental niche-based theory. This study was published in a high-impact journal (*Journal of Ecology*). According to a journal co-editor, it has the potential for great impact on the field of invasion ecology.

However, there was also a gap in knowledge that this study could not address alone. Like most other experimental invasion studies, it ignored the modulating effect of other invasion factors. The experiment was conducted in controlled, homogenous environment (i.e., bare wetland soil; water depth at -3 cm), and at fixed level of seed density (i.e., 3,000 seeds m⁻²). Inevitably, it has limitations regarding implications for

management because fields show much more heterogeneous and complicated conditions than pot experiment. It was necessary to evaluate how biotic resistance is affected by environmental conditions (or abiotic constraints) and propagule pressure.

In Chapter 4, therefore, I investigated how biotic resistance is modulated by abiotic constraints and propagule pressure. I conducted similar pot experiments this time modifying flooding conditions and sowing density, respectively. Then, I applied structural equation models to test hypotheses about cause-effect connections among invasion factors.

Chapter 4 Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion

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4.1. Abstract

With multiple species introductions and rapid global changes, there is a need for comprehensive invasion models that can predict community responses. Evidence suggests that abiotic constraint, propagule pressure, and biotic resistance of resident species each determine plant invasion success, yet their interactions are rarely tested. To understand these interactions, we conducted community assembly experiments simulating situations in which seeds of the invasive *Phragmites australis* land on bare soil along with seeds of resident wetland plant species. We used structural equation models to measure both direct abiotic constraint (here moist vs. flooded conditions) on invasion success and indirect constraint on the abundance, and therefore biotic resistance of resident plant species. We also evaluated how propagule supply of *P. australis* interacts with biotic resistance of resident species during invasion. Flooding always directly reduced invasion success but had synergistic or antagonistic effect on biotic resistance depending on the resident species involved. Biotic resistance of the most diverse resident species mixture remained strong even when abiotic conditions changed. Biotic resistance was also extremely effective under low propagule pressure of the invader, whereas the presence of a dense resident plant cover appears to lower the threshold at which invasion success becomes stable even when propagule supply increases. While our study provides an analytical framework to quantify the effect of multiple interactions relevant to community assembly and species invasion, it also

proposes guidelines for innovative invasion management strategies based on sound understanding of ecological processes.

4.2. Introduction

Biological invasion can be viewed as a community reassembly process for which the outcome depends on multiple interacting factors (Byun et al. 2013; Catford et al. 2009; Sax et al. 2007). In invasion ecology, the need to predict that outcome has led to search for general principles that could guide community conservation, management, or restoration (Heger and Trepl 2003; Kettenring and Adams 2011). Improving predictions of community dynamics, however, remains a challenge. Experimental and analytical frameworks designed to understand and predict the outcome of invasion must take into account not only biotic and abiotic determinants of invasion success individually, but also their interactions (Holle and Simberloff 2005; Perelman et al. 2007; Thomsen et al. 2006b). With multiple species introductions and rapid global changes likely to affect both resident and invading species (Bellard et al. 2013), the need to develop comprehensive invasion models is becoming even more pressing.

Plant invasion is a multi-phase process (introduction, colonization, naturalization, etc.; Dietz and Edwards 2006), and the colonization phase determines whether an invasive species will ultimately establish at a site. For sexually reproducing invaders like *Phragmites australis*, seeds can facilitate long distance spread and rapid colonization of

disturbed sites (Belzile et al. 2010), but seedlings often also represent the most vulnerable stage of plant development (Weisner and Ekstam 1993). Therefore, the colonization phase offers a critical window of opportunities when site or community management can be most efficient if invasive plant control or community restoration is the goal. To achieve these objectives using approaches based on ecological principles, for instance by modifying abiotic conditions and/or by establishing invasion-resistant communities, a good understanding of processes determining the establishment success of invasive species is required.

When anthropogenic or natural disturbances provide opportunities for species recruitment into a community, species will often compete for the available space or resources. Biotic interactions may lead to biotic resistance (Levine et al. 2004), where invading species will be sorted out based on their competitive abilities. The diversity-resistance hypothesis (Elton 1958) predicts that species-rich communities will be more resistant to invasion and experimental studies generally support this hypothesis (Knops et al. 1999; Naeem et al. 2000; Hector et al. 2001; Frankow-Lindberg et al. 2009; Frankow-Lindberg 2012). Not only species richness, however, but also functional group composition in a community can determine the likelihood that a particular invader will colonize a site (Byun et al. 2013; Pokorny et al. 2005). Biotic resistance can reduce the abundance of some invaders, but may not eliminate them entirely (Levine et al. 2004),

as recipient communities are rarely saturated with species (Sax et al. 2007; Tilman 1997). It may, however, keep invaders below nuisance level, thereby reducing the need for extensive interventions.

Biotic resistance may be enhanced by abiotic conditions that filter out intolerant invaders and/or allow the establishment of an invasion-resistant community (Gleason 1926; Melbourne et al. 2007; Weiher and Keddy 1995). Conversely, invaders may be favored by any change in abiotic conditions that are detrimental to resident species, like extreme climatic events for example (Collinge et al. 2011; Goldstein and Suding 2013).

Biotic resistance will also be modulated by propagule pressure (Miller et al. 2013; Thomsen et al. 2006b). Propagule pressure refers to both the number of individual invaders released and the frequency of releasing events to a single location (Lockwood et al. 2005). It remains unclear whether an invader derives increasing benefits from increasing propagule pressure, or whether saturation occurs in a community at a certain propagule threshold (Lockwood et al. 2005). There is therefore considerable interest in relating propagule pressure to invasion success and, even more importantly, to test whether this relationship varies with the seed density of other plant species involved in the community reassembly process or with biotic resistance (Brown and Fridley 2003).

To develop a predictive invasion model, detailed information about how all these abiotic and biotic factors interact under a given set of conditions is required (Herborg et al. 2007; Leung et al. 2012). Although several studies have considered interacting factors in the invasion process (Eschtruth and Battles 2009; Holle and Simberloff 2005; Miller et al. 2013; Perelman et al. 2007; Thomsen et al. 2006b), results are sometimes inconsistent. In some cases, propagule pressure overwhelmingly determines invasion success (Eschtruth and Battles 2009; Holle and Simberloff 2005), while in others abiotic constraints/habitats (Miller et al. 2013; Thomsen et al. 2006b) or biotic factors predominate (Davies et al. 2011). Their relative importance also depends on the scale of investigation (Perelman et al. 2007). Fortunately, recent advances in analytical tools, such as structural equation models (Grace et al. 2010), make it possible to test competing hypotheses regarding interactions and causal relationships among multiple factors in a variety of ecosystems (Whalen et al. 2012). These advances could help improve our ability to predict the outcome of complex invasion process.

In this study, we aim to quantify the interplay between abiotic constraint, propagule pressure, and biotic resistance in the critical colonization phase of the invasion process. Our target invader is *Phragmites australis* (Cav.) Trin. ex Steud., a widely spread grass (Poaceae) with at least one introduced lineage in North America (haplotype M in this case) (Kettenring et al. 2012; Meyerson et al. 2010; Saltonstall 2002). The introduced *P.*

australis is aggressively invading wetlands and anthropogenic linear habitats such as roadside or agricultural ditches (Brisson et al. 2010; Maheu-Giroux and de Blois 2007; Moody and Mack 1988). We conducted two experiments simulating a situation in which *P. australis* seeds land on bare soil along with other wetland plant species, a common occurrence in the field after disturbances. For the species-environment experiment, we expected biotic resistance (measured as decrease in invasion success of *P. australis*) to vary depending on the identity and diversity of other resident wetland plants involved in the assembly process. We also tested a series of hypotheses about the ways abiotic conditions (here moist vs flooded conditions) modulate biotic resistance. For the propagule experiment, we evaluated the interactions between propagule pressure of *P. australis* and seed density of resident wetland plants in determining biotic resistance.

4.3. Materials and methods

We conducted two outdoor pot experiments at the Montreal Botanical Garden (Quebec, Canada) (1) a species-environment experiment in 2010 and (2) a propagule experiment in 2011. Fertile clay soil was collected from natural wetlands for use in both experiments and sterilized with a steam pasteurizer at 76 °C for 4 hours to kill any viable seeds and prevent unwanted contamination. The pots (diameter 25.4 cm, height 30.5 cm) were immersed in water using large plastic containers (6 pots per container). In the species-environment experiment, water level was maintained constant with an automatic water

gauge device at either 5 cm below soil surface in the pot (hereafter referred to as moist conditions) or 5 cm above soil surface (hereafter referred to as flooded conditions).

Bricks were used to raise the pots to the height required for moist conditions (Appendix 4-1).

Species selection

Anaerobic tolerance should be a good indicator of resistance to flooding, the main abiotic constraint in our experiment. As for several other species, the anaerobic tolerance of *P. australis* varies according to its developmental stages, with relatively low tolerance at seedling stage but increasing tolerance with age (Engloner 2009; Mauchamp et al. 2001). We chose five other wetland plant species commonly found in the area and covering a range of anaerobic tolerance levels at maturity to test biotic resistance in the experiments (hereafter referred to as resident species - Appendix 4-2).

Typha latifolia L. (Typhaceae) has high anaerobic tolerance. Both *Panicum virgatum* L. (Poaceae) and *Scirpus cyperinus* (L.) Kunth (Cyperaceae) have intermediate tolerance. *Eutrochium maculatum* (L.) E.E. Lamont (Asteraceae) and *Lolium multiflorum* Lam. (Poaceae) have the lowest anaerobic tolerance of all species at maturity. This range allowed us to test hypotheses about the interplay between biotic resistance and abiotic conditions assuming differences in anaerobic tolerance among species determine in part their response to abiotic constraints (here their cover in moist vs. flooded

conditions) and therefore could modulate their biotic resistance under different environmental conditions. We used accepted species name as reported in VASCAN, the Database of Vascular Plants of Canada (Brouillet et al. 2010+).

Prior to the experiments, seeds of *P. australis* were collected from mature colonies of the exotic genotype thriving in roadside ditches in Dundee, Quebec, Canada (N 45°05'50.6", W 74°24'36.4"). Seeds of *T. latifolia* were collected from a naturally established colony at the Montreal Botanical Garden. Seeds of other resident species were purchased from seed suppliers, and had been harvested from an identified ecotype in natural habitats in North America. We standardized seed viability among species by applying pure live seed rates as determined by our own test (for *P. australis* and *T. latifolia*) or from information provided by the suppliers for the other species.

Species-environment experiment

In the species-environment experiment, we applied two-way factorial design to test both main and interaction effects of treatments. For each water level (either moist or flooded), we planted seeds, varying species composition as follows: Control (only *P. australis*), 2-species mixtures (each of the 5 resident species individually + *P. australis*) and 6-species mixture (all 5 resident species + *P. australis*) based on an additive competition design (Connolly et al. 2001). Each treatment was replicated 3 times in a

randomized complete block design (one replicate per block) for a total of 42 experimental units. Seed density of the resident species was fixed at 140 pure live seeds per pot regardless of the number of resident species; it was equally distributed among all 5 resident species (28 seeds per species) in the case of the 6-species mixture. We used the same sowing density (140 pure live seeds) for *P. australis* for a total of 280 pure live seeds per pot. This corresponds to roughly 4,000 seeds m⁻², which is within the range of seedbanks from natural wetlands (Galatowitsch and van der Valk 1996). All seeds, including those of *P. australis*, were cold-stratified at 3°C until sown. We ran this experiment from May to October 2010.

Propagule experiment

In the propagule experiment, we evaluated the interaction between propagule supply of *P. australis* and biotic resistance of resident species by varying both seeding density of *P. australis* and of resident species, while water level and resident species identity were fixed. Increasing propagule pressure from *P. australis* should increase invasion success, while increasing resident species cover should increase biotic resistance and therefore decrease invasion success. We used a mixture of *T. latifolia* and *L. multiflorum* in equal proportion for the resident species because these species had shown good resistance to invasion in the first experiment. Water level was kept at intermediate level (2 cm below soil surface) to minimize abiotic constraint. For seeding

density of *P. australis*, treatments were as follow: 30, 90, 300, or 900 seeds. For the two resident species, treatments were as follow: no seed, 90 or 450 seeds. All species were sown in pots (diameter 15.2 cm, height 12.7 cm) using a factorial design. Seeding density treatments were replicated 3 times for a total of 36 experimental units, and the pots were allocated in a randomized complete block design. We ran this experiment from May to October 2011.

Data collection

At the end of the growing season for both experiments, we counted the number of *P. australis* shoots to quantify invasion success. We also measured cover (%) of the resident species using the point intercept method with a 40-cell mesh. Plant cover was considered an appropriate measure to compare species with different life forms and sizes and it was used, in this case, to relate the abundance of a resident species to its biotic resistance (i.e., the effect of resident species on invasion success) in structural equation models. For the 6-species mixture, plant cover included all resident species.

Data analyses

Two-way ANOVA was used to test the main effect of each treatment as well as their interaction effect. The generalized linear mixed model with REML for the ANOVA test was applied, taking into account random block effect (Bolker et al. 2009). When

significant main effects were found, we compared means using Tukey's HSD multiple comparison test. In all analyses, the assumptions of normality of residuals and homoscedasticity were checked, and response variables were log-transformed to meet the assumption if necessary. In addition, we used regression analysis to test the relationship between cover of resident species and number of *P. australis* shoots.

In the species-environment experiment, structural equation models (Grace 2006; Grace et al. 2010; Grace et al. 2012) were used to test further hypotheses about causal relationships, as we found significant correlations among factors in two-way ANOVA. Structural equation models allow untangling direct and indirect effects of water level and resident species cover on invasion success (see Figure 4-1 and Box 1 for details). To illustrate, flooding can have an effect on an invader as well as on a resident species cover. The former is considered in our models as a direct effect of flooding on invasion success, whereas the latter, by reducing or increasing the cover of resident species, as an indirect effect on invasion success through biotic resistance. Different chains of causal relationships, given different combinations of direct and indirect effects, correspond to alternative hypotheses about mediation patterns (Box 1).

We built the models using *sem* function in the *lavaan* R package with maximum likelihood, then compared goodness of model fit using AICc (corrected Akaike

information criterion) and Akaike weight in a model selection approach (Burnham et al. 2002; Johnson and Omland 2004). We calculated AICc and Akaike weights using *aictab.lavaan* functions in the *lavaan* package. In general, a lower AICc means a better model fit (significant when $\Delta AICc > 2$). Akaike weights (w_i) can be viewed as the probability that model i is the best model given a set of competing model candidates (Johnson and Omland 2004). After choosing the best model, we estimated standardized value of covariance on each connection of interests (dotted line in our model system; Figure 4-1). We used JMP software (© SAS) for the classical statistical tests (ANOVA and regression analysis) and for drawing figures. We used R software (www.r-project.org) to build the structural equation models and to compare models' goodness of fit.

Box 1 Structural equation models with hypotheses

A structural equation model typically involves multiple equations each representing hypotheses about causal relationships and mediation patterns in a system.

Let's assume that a response variable y_1 is influenced by another variable x_1 :

$$x_1 \rightarrow y_1 \text{ or } y_1 = f(x_1)$$

In addition, x_1 may also affect another response variable of interest y_2 directly, or indirectly through y_1 . In this case, we will say that the response of y_2 is determined by both the direct effect of x_1 and indirect effect of x_1 mediated by y_1 .

$$x_1 \rightarrow y_1 \rightarrow y_2 \text{ or } y_2 = f(x_1, y_1)$$

Structural equations are expressed in classical simple linear models to express different pathways of causal relationships.

$$y_1 = \alpha_1 + \gamma x_1 + \zeta_1$$

$$y_2 = \alpha_2 + \gamma x_1 + \beta y_1 + \zeta_2$$

Our species-environment experiment is more complex, with the main response variable being invasion success (y_2 - number of shoots of *P. australis*). The mediator variable, resident plant cover (y_1), provides an indication for biotic resistance (i.e., the effect of resident species on invasion success). Both can depend on water level (x_1 ; 0 - moist or 1 - flooded) and whether or not resident species were sown (x_2 : 0 - no seed/control; 1 - seeded). Equations reflect the fact that both direct and indirect effects can be significant (partial mediation), that only direct effects are significant (no mediation), or that only indirect effects are significant (complete mediation). We built and tested separate models for each species mixture type and compared the results for the different resident species mixtures.

SEM 1 (partial mediation model; equation 1)

Hypotheses: *P. australis* invasion success depends on abiotic constraints (water level) both on the invader and on resident species. Hence biotic resistance depends on abiotic

conditions and may vary with resident species' response to water level (presumably related to their anaerobic tolerance).

$$y_1 = \alpha_1 + \gamma_2 x_1 + \gamma_3 x_2 + \zeta_1$$

$$y_2 = \alpha_2 + \gamma_1 x_1 + \beta_1 y_1 + \zeta_2 \quad \text{eqn 1}$$

where y_1 = resident plant cover (%), y_2 = number of shoots of *P. australis* (invasion success); x_1 = water levels (moist or flooded); x_2 = seed treatments (no seed or seeded); γ_1 = correlation coefficient between water level (x_1) and invasion success (y_2) as an indicator for direct flooding effect on invasion; γ_2 = correlation coefficient between water levels (x_1) and resident plant cover (y_1) as an indicator for flooding effect on resident plants; γ_3 = correlation coefficient between seed treatments (x_2) and resident plant cover (y_1); β_1 = correlation coefficient between resident plant cover (y_1) and invasion success (y_2) as an indicator for biotic resistance; ζ (zetas) are residuals (see also Figure 4-1).

SEM 2 (no mediation model; equation 2)

Hypotheses: *P. australis* invasion success depends on abiotic constraints (water level) on the invader and on biotic resistance from the resident species. The performance of the latter, however, does not depend on abiotic conditions (in equation SEM 1, either $\gamma_2=0$ or $\beta_1=0$).

$$y_1 = \alpha_1 + \gamma_3 x_2 + \zeta_1$$

$$y_2 = \alpha_2 + \gamma_1 x_1 + \beta_1 y_1 + \zeta_2 \quad \text{eqn 2}$$

SEM 3 (complete mediation model; equation 3)

Hypotheses: *P. australis* invasion success depends only on biotic resistance to invasion as determined by abiotic constraints. There is no direct effect of water level on the invader (in the equation of SEM 1, $\gamma_1=0$)

$$y_1 = \alpha_1 + \gamma_2 x_1 + \gamma_3 x_2 + \zeta_1$$

$$y_2 = \alpha_2 + \beta_1 y_1 + \zeta_2 \quad \text{eqn 3}$$

4.4. Results

Species-environment experiment

Abiotic constraints and biotic resistance interactively determined *P. australis* invasion success (Figure 4-2). Both water level and resident species treatments were significant (Two-way ANOVA test on log-transformed y: main effect of water level: $F_{1,32}=21.94$, $P<0.001$; resident species treatments: $F_{6,32}=14.96$, $P<0.001$). *Phragmites australis* invaded less in flooded (average shoots of *P. australis* per pot, $\bar{y}=121$) than in moist conditions ($\bar{y}=176$). *Phragmites australis* invasion was lowest with the 6-species mixture ($\bar{y}=50$), followed by the 2-species mixtures of *L. multiflorum* ($\bar{y}=75$), *T. latifolia* ($\bar{y}=124$),

P. virgatum ($\bar{y}=155$), *S. cyperinus* ($\bar{y}=185$) and *E. maculatum* ($\bar{y}=204$) in that order.

There was a significant interaction effect between water level and resident species treatments and *P. australis* invasion (log-transformed y ; $F_{6,32}=4.22$, $P=0.003$). While *L. multiflorum* resisted *P. australis* invasion much better in moist than flooded conditions, *T. latifolia* resisted the invasion better in flooded than in moist conditions. *Phragmites australis* invasion success decreased as resident species cover increased in a linear relationship both in moist ($F_{1,22}=52.62$; $P<0.001$; equation 4) and in flooded ($F_{1,22}=31.30$; $P<0.001$; equation 5) conditions (Appendix 4-3).

$$y_2=251.9 - 2.54 \cdot y_1 \quad \text{eqn 4}$$

$$y_2=156.0 - 1.55 \cdot y_1 \quad \text{eqn 5}$$

where y_1 stands for resident species cover (%) and y_2 stands for number of *P. australis* shoots per pot. *Phragmites australis* invasion success was negatively correlated with resident species cover in moist conditions (Pearson correlation coefficient, $r=-0.83$) and in flooded conditions ($r=-0.76$). In a further ANOVA test, both water level and species composition significantly affected resident species cover (log-transformed y ; main effect of water level: $F_{1,32}=28.63$; $P<0.001$; species: $F_{6,32}=155.7$, $P<0.001$) with significant interactions (log-transformed y ; $F_{6,32}=33.58$; $P<0.001$). Resident species with low anaerobic tolerance, such as *L. multiflorum* and *E. maculatum*, were more abundant in moist than in flooded conditions, while *T. latifolia*, with high anaerobic tolerance, was more abundant in flooded than in moist conditions. The abundance of *P. virgatum* and,

interestingly, of resident species growing in the 6-species mixture did not vary significantly with water level.

Table 4-1 compares the SEM results for the different species mixtures. For most 2-species mixtures, the partial mediation model (SEM 1; having both direct effect of abiotic constrains on invasion success and indirect via resident species cover) was the best model (with lowest AICc). In the cases of the 2-species mixture with *P. virgatum* and of the 6-species mixture, the null mediation model (SEM 2; only direct effect on *P. australis*, no mediation) had the lowest AICc, but its goodness of fit was not significantly better than SEM 1 (Δ AICc <2). While the direct effect of flooding on *P. australis* invasion was significantly and consistently negative, flooding had different effect on biotic resistance depending on the resident species in the 2-species mixtures (Figure 4-3). For instance, while biotic resistance from *L. multiflorum* reduced *P. australis* invasion success ($\beta=-0.85$), flooding also reduced *L. multiflorum* cover ($\gamma_2=-0.19$). The indirect flooding effect on invasion, mediated by effect on *L. multiflorum* cover, was estimated at 0.16 (= -0.19×-0.85). Therefore, flooding prevented biotic resistance from *L. multiflorum*. In contrast, flooding increased *T. latifolia*'s abundance ($\gamma_2=0.32$), while biotic resistance from *T. latifolia* reduced invasion ($\beta=-0.48$). The indirect flooding effect on invasion, mediated by effect on *T. latifolia* cover, was estimated at -0.15 (= 0.32×-0.48). Therefore, flooding enhanced *T. latifolia*'s biotic resistance. For *P. virgatum* and

the 6-species mixture, flooding effect ($\gamma_2=-0.02$ and -0.03 , respectively) on their abundance was marginal. Their biotic resistance was not significantly influenced by water level in this study. For *E. maculatum* and *S. cyperinus*, flooding reduced their abundance ($\gamma_2=-0.41$ and -0.38), as for *L. multiflorum*, but their biotic resistance was marginal or ineffective ($\beta=-0.15$ and -0.10). In these cases, *P. australis* invasion success was controlled mostly by direct flooding effect on *P. australis*, i.e., neither by mediation nor biotic resistance. All resident species mixtures could thus be arranged along gradients of response to flooding and biotic resistance (Appendix 4-4).

Propagule experiment

Both propagule supply of *P. australis* and seeding density of resident species had significant effects on invasion success (Figure 4-4; two-way ANOVA test: propagule pressure: $F_{3,22}=14.03$, $P<0.001$; seeding density of resident species: $F_{2,22}=38.21$, $P<0.001$). *Phragmites australis* invasion success increased with propagule supply, but decreased with seeding rate of resident plants. In addition, there were significant interactions between propagule supply and seeding density of resident plants ($F_{6,22}=7.46$, $P<0.001$). The effect of seeding density of resident plants on the relationship between propagule supply and invasion success suggests that there are clear benefits in investing in a dense cover of resident species, especially under low propagule pressure (Appendix 4-5a, b). Biotic resistance stopped invasion when

propagule supply was the lowest (30 seeds pot⁻¹) and reduced invasion even under high propagule pressure when a resident plant cover was present compared to no cover.

Conversely, invasion success increased with propagule pressure most rapidly and to its highest level when there was no cover.

4.5. Discussion

Our study examined how biotic resistance, abiotic constraint, and propagule pressure interactively regulate *P. australis* invasion and identified synergetic or antagonistic processes relevant to community assembly and management. Biotic resistance varies with the identity and diversity of wetland plant species in the community and is also modulated by abiotic conditions, in relation to resident species traits or propagule pressure. Structural equation models support a partial mediation hypothesis in which *P. australis* invasion success depends on abiotic constraints (water level) both on the invader and on resident species.

The strength of biotic resistance to invasion is determined by various components of a community, including dominant species identity (Emery and Gross 2007; Sheley and James 2010), species diversity (Fargione and Tilman 2005; van Ruijven et al. 2003), functional group identity (Byun et al. 2013; Fargione et al. 2003), and functional diversity (Pokorny et al. 2005). Direct indicators of biotic resistance are also provided by resident

species' performance traits or community-wide fitness, such as plant size (Schamp and Aarssen 2010), plant cover (this study; Gerhardt and Collinge 2003), height (Gaudet and Keddy 1988) or biomass (Gaudet and Keddy 1988; Lulow 2006; Rinella et al. 2007). Interestingly, total plant cover of the 6-species mixture was relatively stable in both flooded and moist conditions. In this mixture, niche partitioning (or complementarity) among species each adapted to certain conditions or with different traits contributed to maintaining community-wide abundance even when conditions changed. Such community-wide stability could secure invasion resistance, evoking the insurance hypothesis (Ives et al. 2000; Loreau et al. 2001; Tilman et al. 2006; Byun et al. 2013).

Biotic resistance was partially modulated by flooding. Abiotic constraints and biotic resistance have been shown to determine invasibility when conditions varied in terms of water depth (Collinge et al. 2011; Gerhardt and Collinge 2003), sediment salinity (Dethier and Hacker 2005), or soil nutrients (Goldstein and Suding 2013). We provide additional quantitative evidence that biotic resistance and abiotic constraints work synergistically (or antagonistically) to control invasion depending on species traits in the species pool. In stressful or harsh environments, abiotic constraints alone can determine the fate of invaders (Chytrý et al. 2008; Dethier and Hacker 2005; Wang et al. 2006), as shown by the lower abundance of *P. australis* in flooded conditions compared

to moist conditions in this study. Abiotic stress, however, can also determine the abundance of resident wetland plants, and therefore indirectly modulate their potential to offer biotic resistance. Most resident species were less abundant when flooded, except for *Typha latifolia*. The outcome of strong abiotic filtering has been shown to result in trait underdispersion and phylogenetic clustering during community reassembly (Adler et al. 2013; Procheş et al. 2008). The direct benefit of biotic resistance on invasion is expected to be more significant in benign or intermediate conditions that favor a broad range of species (Gerhardt and Collinge 2003; Naeem et al. 2000; Perelman et al. 2007; Thomsen et al. 2006a; Thomsen et al. 2006b), the moist conditions in our case. In these conditions, species can express their differential potential for invasion resistance depending on species traits and can therefore be ranked from most to least resistant to invasion accordingly.

The ability to predict the outcome of the interplay between abiotic constraints and biotic resistance on biological invasion in any given set of conditions rests on a good knowledge of the functional ecology of species. Our experiments illustrate the importance of fitness-related traits (how well a species adapts to given abiotic constraints) for species to resist invasion. Sharing information about species through databases of functional traits such as TRY (Kattge et al. 2011) should facilitate the

rigorous testing of specific predictions about community responses to invasion (Heger and Trepl 2003).

The invasion success of *P. australis* increases with propagule pressure, but there may be a threshold, or at least a saturation tendency, beyond which additional *P. australis* seeds will not necessarily increase invasion proportionally. Interestingly, our results suggest that biotic resistance from a resident plant cover could lower that threshold, with potential benefits in terms of community dynamics and control. The decision to invest or not in the restoration of a competitive cover may depend on how these benefits are perceived. For instance, reducing invasion success early in community assembly may have long term benefits in terms of the frequency and cost of control interventions if invader populations stabilize at manageable levels. Dense communities typically offer fewer opportunities for invaders' establishment than sparse or disturbed ones (Lindig-Cisneros and Zedler 2002a). Density could therefore be just as important as the species richness of the resident community in determining invasibility, particularly in the early establishment phase (Brown and Fridley 2003; Meiman et al. 2009; Reinhardt Adams and Galatowitsch 2008). Under the highest propagule pressure, biotic resistance offered by a dense cover of resident plants (450 seeds pot⁻¹) reduced invasion by 93% on average compared to control. A dense plant cover consisting of 6 species in the canopy cover and one species in matrix cover reduced invasion of *Phalaris arundinacea* (reed

canary grass) by 98.1%, compared to 77% under sparse cover (Lindig-Cisneros and Zedler 2002b). Other studies have found a significant interaction between abiotic constraint and propagule pressure, suggesting that alleviating abiotic constraint/stress promote seed establishment under a given level of propagule pressure (Adler et al. 2013; Thomsen et al. 2006b). Overall, biotic resistance reduced invasion success significantly and effectively; biotic resistance alone, however, does not guarantee complete suppression of recruitment. Under high propagule pressure, raising water level may further prevent invasion, as shown in our study, providing that some of the resident species in the mixture can tolerate the changes in abiotic conditions, hence the importance of species diversity.

Introduced *P. australis* is considered an invasive species in many wetland ecosystems in North America and efforts to eradicate it are ongoing, often at high costs and with repeated interventions. Very few experimental studies so far have rigorously evaluated the role of resident plant communities in preventing or delaying reinvasion when control is done or when a wetland is disturbed. In these cases, our study shows that the outcome of community reassembly and invasion success will depend on the interactions between wetland plant identity/diversity, abiotic conditions, and propagule pressure. The ability of a species to provide biotic resistance will vary with abiotic conditions, and therefore, mixtures of species are more likely to provide reliable resistance services in

fluctuating environmental conditions—a common situation in wetlands—than monocultures. The positive effect of propagule pressure on invasion success may be offset by dense communities of invasion-resistant species that occupy available niches. Although complete eradication through biotic resistance is unlikely, avoiding or delaying the establishment of a dense *P. australis* cover could be beneficial. Finally, while species selection depends on the ecosystem under consideration, we believe that the principles outlined in this study are robust enough to provide insights on community assembly and invasion process in any system.

4.6. Tables

Table 4-1: Selection of the best structural equation models (SEM 1-3) for the species-environment experiment. The models test hypotheses about direct and indirect effects of flooding on invasion success of *P. australis* given the resident species present. The mixture refers to all 5 resident species. SEM 1: partial mediation - both direct flooding effect and indirect flooding effect through resident species. SEM 2: null mediation - direct effect only. SEM 3: complete mediation- indirect effect only. K = number of model parameters. Asterisks indicate best model for a given species treatment with corrected Akaike information criterion and Akaike weight shown. Models in bold are not significantly different from the best model for that treatment ($\Delta AICc < 2$)

Models	K	<i>Lolium</i>	<i>Typha</i>	<i>Panicum</i>	<i>Scirpus</i>	<i>Eutrochium</i>	Mixture
SEM 1	8	372, 0.83*	439, 0.82*	371, 0.16	410, 0.84*	415, 0.84*	430, 0.20
SEM 2	7	375, 0.17	442, 0.18	369, 0.84*	414, 0.16	418, 0.16	428, 0.75*
SEM 3	7	386, 0.00	451, 0.00	382, 0.00	424, 0.00	426, 0.00	433, 0.05

4.7. Figures

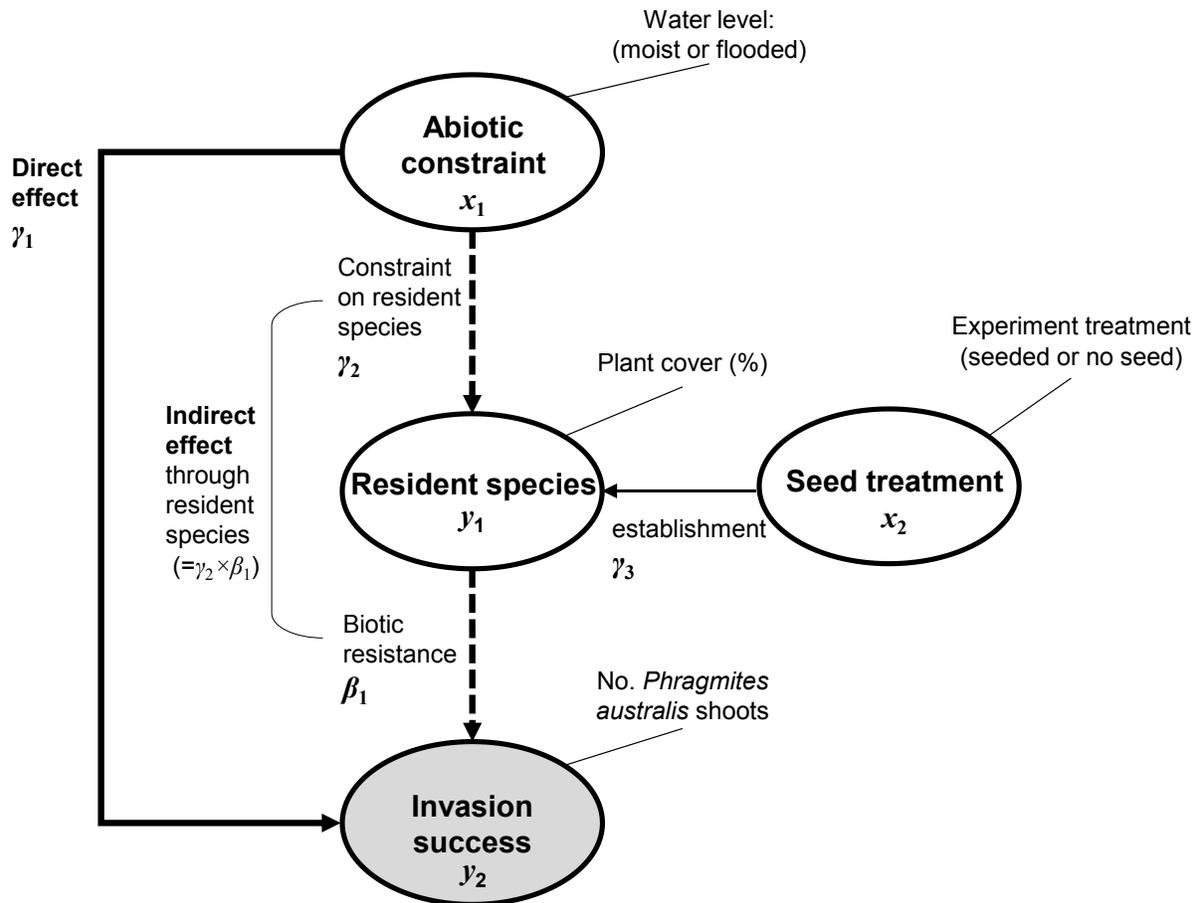


Figure 4-1: Diagram showing proposed causal relationships among factors hypothesized to affect *P. australis* invasion success in the species-environment experiments. Abiotic constraint (flooding) can have both direct (solid line) and indirect (dashed lines) effects on invasion success. Resident plant species may offer biotic resistance. See Table 4-1 for the details of the structural equation models

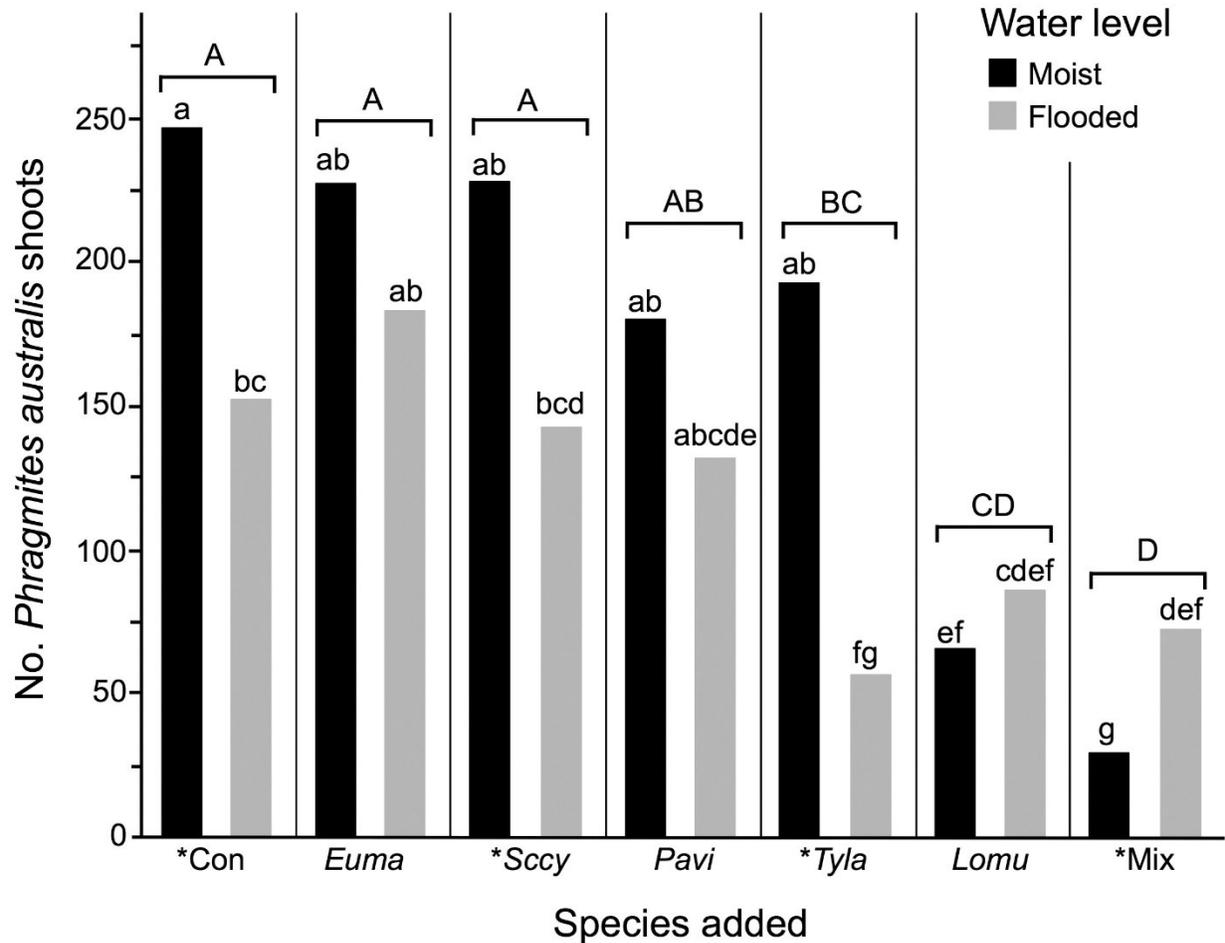


Figure 4-2: Effect of biotic resistance from resident species on *P. australis* invasion success at two water levels. Con = Control; no resident species added; Mix = Mixture; all 5 resident species added (Euma=*Eutrochium maculatum*; Sccy = *Scirpus cyperinus*; Pavi = *Panicum virgatum*; Tyla = *Typha latifolia*, and Lomu = *Lolium multiflorum*). Species treatments with the same upper case letter do not significantly differ from each other (Tukey's HSD test; $P > 0.05$). Combinations of water level/species treatments with the same lower case letter do not significantly differ from each other (Tukey's HSD test; $P > 0.05$). Asterisks indicate significant differences between water levels within each species treatment (contrast test; $P < 0.05$)

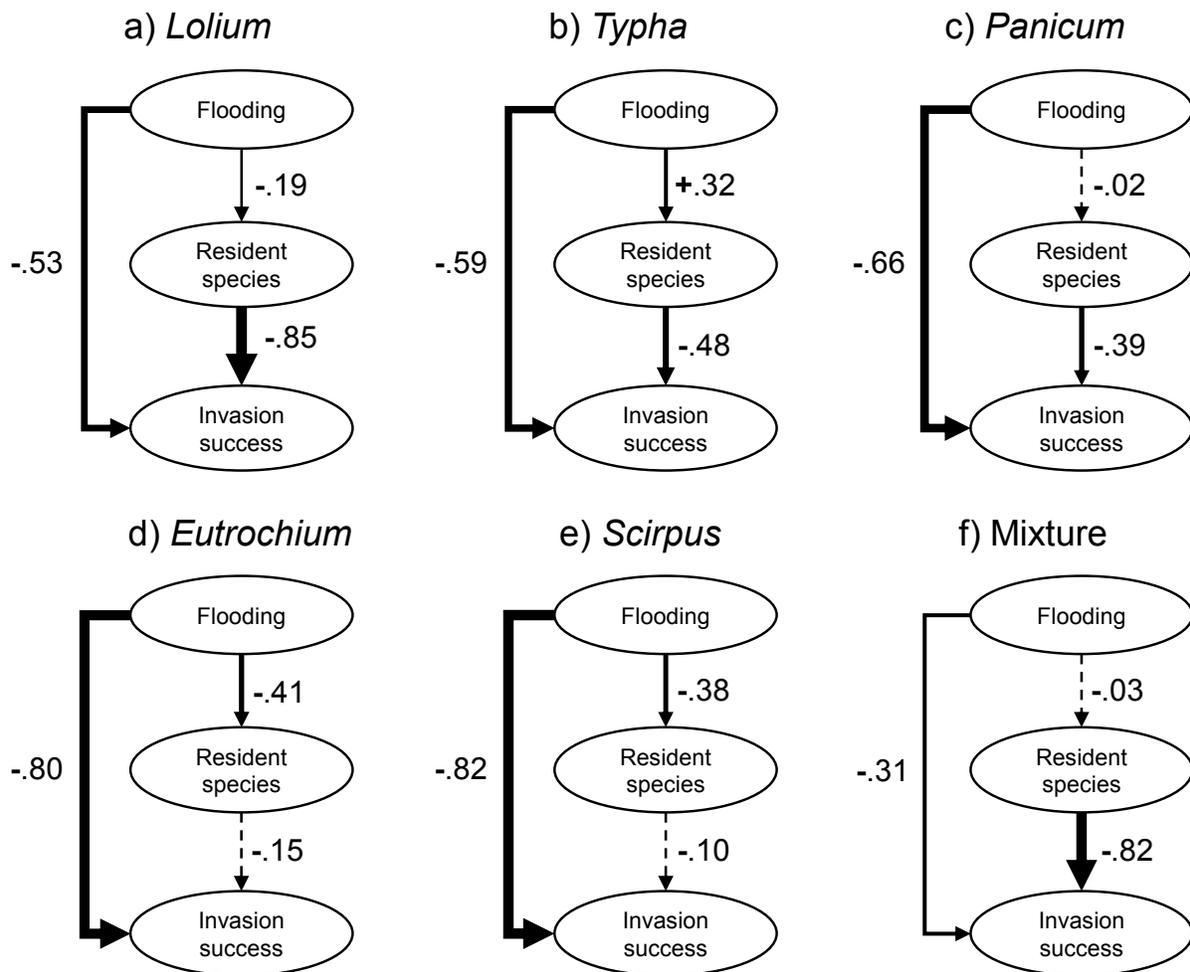


Figure 4-3: Structural equation model results (SEM 1: partial mediation) for each species composition (a) *Lolium multiflorum* (b) *Typha latifolia*, (c) *Panicum virgatum*, (d) *Scirpus cyperinus*, (e) *Eutrochium maculatum*, and (f) mixtures of 5 species. Numbers are standardized parameter values for the relationship of covariance with sign indicating positive or negative effect. Solid lines represent significant effect (t test; $P < 0.05$); bar width indicates magnitude of effect. Dashed lines represent non-significant effect ($P > 0.05$)

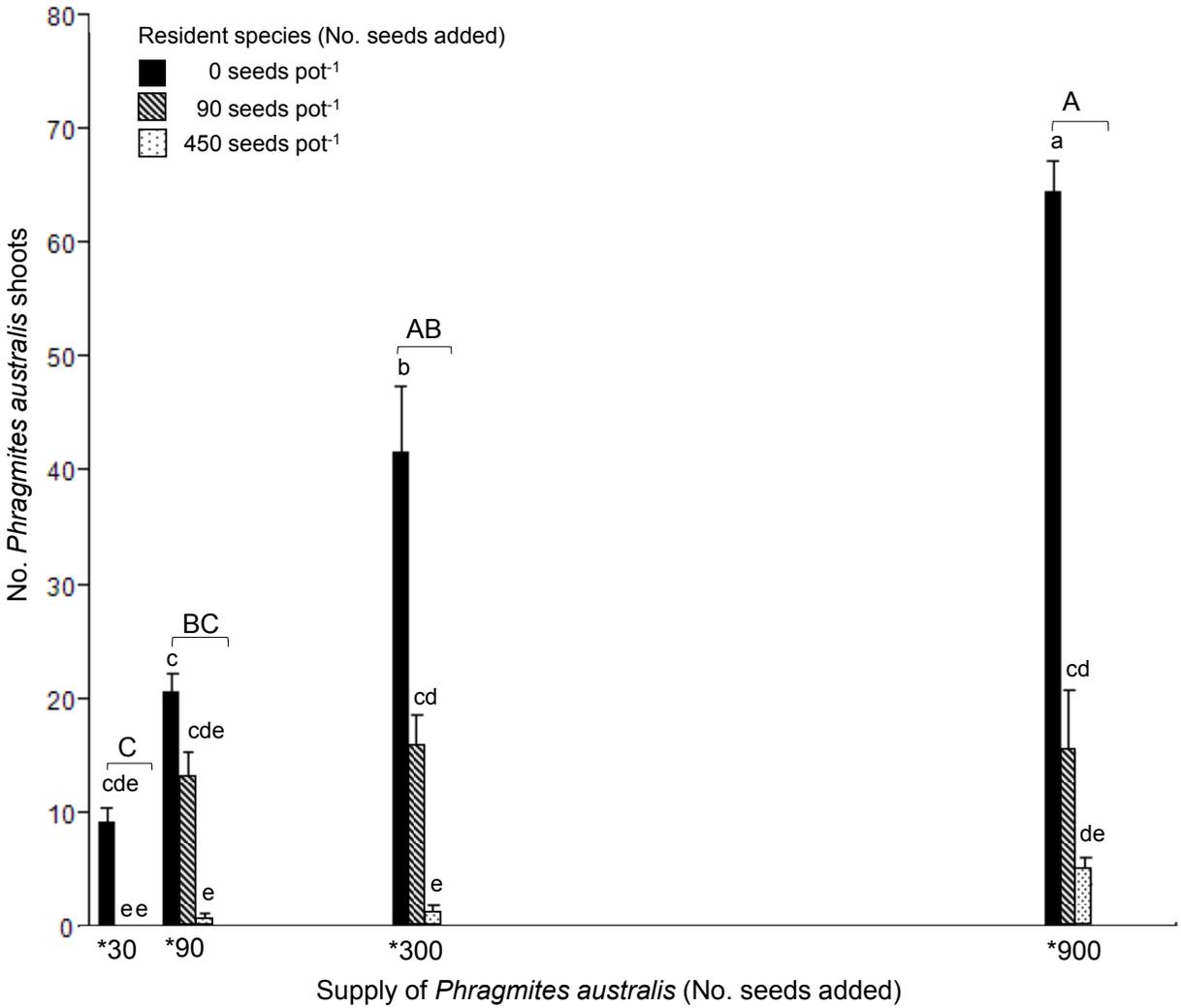


Figure 4-4: Effect of propagule supply of *P. australis* on invasion success at three seeding densities of resident species. Propagule supply treatments with same upper case letter do not significantly differ from each other (Tukey's HSD test; $P > 0.05$). Combinations of propagule supply/seeding density treatments with same lower case letter do not significantly differ from each other (Tukey's HSD test; $P > 0.05$). Asterisks indicate significant differences among seeding densities of resident plants within each propagule supply treatment (contrast test; $P < 0.05$)

4.8. Connections to the next Chapter

In Chapter 4, I investigated on interaction between biotic resistance and either abiotic constraints or propagule pressure. The species-environment experiment shows that abiotic constraint and biotic resistance synergistically or antagonistically work in controlling invasion depending on the recipient species' fitness to given environmental condition. Relatively consistent total plant cover of mixtures across water level implies niche partitioning and insurance effect. In addition, the propagule experiment shows that sowing density of a recipient community can limit the threshold in the effect of propagule pressures on invasion success. In synthesis of two experiments bring us an insight that there is dynamic interplay among invasion determinants, therefore one should consider these relationships to combine species mixture as restoration practices to produce synergetic effects.

While my second study provides ecological guidelines how to restore plant communities depending on given abiotic condition to control *P. australis*, the both of two studies (Chapter 3 and 4) are conducted in small-scale microcosm experiment. Scaling up to a field situation enable us to fully taking into account (1) multiple invaders are naturally-dispersed from nearby meta-communities and recruited into plant community (e.g. major invaders include *Phragmites australis*, *Salix alba*, *Populus tremuloides*, and etc.), (2) maximizing diversity levels (from 4 to 8, 16 species), (3) full, random mixtures of four

functional groups, and while (4) addressing *in situ* environmental condition as a covariant (e.g., flooding %). This synthesized study addressed multiple mechanisms underlying diversity-invasibility using advanced diversity-interaction models and multi-model inference.

Chapter 5 Diversity reduces invasion through functional group interactions
in plant community reassembly

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5.1. Abstract

Contradictory patterns in diversity-invasibility relationship across communities and scales suggest multiple drivers interact in the invasion process. We investigated species interaction mechanisms underlying diversity-invasibility accounting for the influence of multiple drivers.

We conducted a large field experiment in a wetland basin under high propagule pressure from *Phragmites australis* and other naturally dispersed species. We manipulated species diversity and functional group composition in applied seed mixtures and measured abundance of invaders as response variable. We built diversity-interaction models using structural equations and model selection to identify primary resistance mechanisms.

We found that diverse communities are more resistant to multiple invaders mainly due to interactions between functional groups, suggesting life history trade-offs and resource partitioning via functional complementary. The selection effect of certain functional groups and flooding effect were also significant but invader-specific. By embracing multifaceted invasion processes, this study brings new insights into community reassembly mechanisms relevant to ongoing ecological changes.

5.2. Introduction

With unprecedented rates of species introductions, human disturbances, and rapid global warming, a broad scale reorganization of species within communities is to be expected. Yet, our understanding of how species interact in a variable environment to make communities more or less resistant to invasion remains surprisingly limited. Ever since Charles Elton proposed that more diverse communities would be less susceptible to invasion or more resilient to changes, there has been a search for overarching principles in invasion ecology and community assembly (Fridley et al. 2007).

Apparent contradictory patterns in diversity-invasibility relationships, however, emerged across communities and scales (Levine 2000, Fridley et al. 2007): negative relationship at local scale (Tilman 1997, Kennedy et al. 2002, Frankow-Lindberg et al. 2009e, Frankow-Lindberg 2012) and positive relationship at regional scale (Stohlgren et al. 2003, Davies et al. 2005, Melbourne et al. 2007). This made it evident that, beyond the search for generalized patterns, a better understanding of processes and mechanisms driving complex community and invasion dynamics was needed (Ives and Carpenter 2007).

We suggest that a promising, yet largely unexplored avenue is to use an integrated approach, facilitated by advances in analytical tools, to investigate functional

mechanisms underlying species interactions that contribute most to biotic resistance to invasion. Such an approach must explicitly recognize the complexity and scale dependency of diversity-invasibility relationships (Fridley et al. 2007), as well as the interplay between propagule pressure (Lockwood et al. 2005), environmental heterogeneity (Davies et al. 2005, Melbourne et al. 2007), and biotic resistance (Levine et al. 2004) that ultimately determine invasion patterns (Catford, Jansson & Nilsson 2009; Chapter 4).

Diversity effect, recognized as one of the main drivers of biotic resistance to invasion, can be partitioned into complementarity diversity effect and selection effect (Loreau and Hector 2001). Complementarity diversity effect can be significant if resource partitioning, or positive interaction between species, most contributes to net diversity effect (Levine and D'Antonio 1999, Kennedy et al. 2002, Levine et al. 2004). In relation with the niche, a theory of diversity-resistance posits that diverse communities have less unused niche space, preventing invasion (Kennedy et al. 2002, MacDougall et al. 2009). Niche partitioning can be indicated by increasing number of neighboring plants (Kennedy et al. 2002) or canopy complexity (Lindig-Cisneros and Zedler 2002a), or partitioning resource uptakes (Booth et al. 2003, Frankow-Lindberg 2012). A related theory of fluctuating resources availability postulates that invaders will take advantage of short-term increases in available resources unused by local communities (Davis et al. 2000).

Functional traits of species are related to their niche and fitness dimension (McGill et al. 2006) and, therefore, if traits of species in a community are well dispersed over available niche space, such community may leave fewer resources available for potential invaders (Funk et al. 2008). In this regard, functional group diversity could be more directly indicative of complementarity diversity effect on invasion resistance than species diversity (Symstad 2000, Pokorny et al. 2005) but see also (Prieur-Richard et al. 2000).

Selection effect (or sampling effect), on the other hand, can be significant if certain species included in communities mostly influence diversity effect (van Ruijven et al. 2003, Emery and Gross 2007). Functional group identity (proportion of certain functional group in a community) can influence invasion resistance (Prieur-Richard et al. 2000, Fargione et al. 2003, Fargione and Tilman 2005, Mwangi et al. 2007, Price and Pärtel 2013), although there are exceptions (Von Holle and Simberloff 2004). Fox's assembly rule hypothesizes that the lack of a certain functional group in a community will facilitate invasion by that particular functional group (Von Holle and Simberloff 2004). In some case, a functional group that is similar to that of a potential invader offers more resistance to that invader (Fargione et al. 2003, Fargione and Tilman 2005), supporting Fox's assembly rule. In other cases functional groups different from invaders resist most (Symstad 2000, Lulow 2006, Sheley and James 2010, Byun et al. 2013), suggesting

that fitness difference (driving competitive dominance) determines resistance (MacDougall et al. 2009).

Growing empirical evidence indicates that both complementarity and selection effect can contribute to net diversity effect on invasion resistance (Fargione and Tilman 2005, Frankow-Lindberg et al. 2009e); little is known, however, about their relative contribution. Furthermore, different mechanisms may affect invasion resistance depending on the diversity of invaders. For instance, Funk et al. (2008) hypothesized that communities showing functional redundancy would be more resistant to a particular type of invader, while complementarity may offer resistance to a wider range of invaders.

These recent advances in community theory, combined with novel analytical tools such as diversity-interaction models based on structural equations (Kirwan et al. 2009, Connolly et al. 2013) and functional trait-based framework (McGill et al. 2006, Funk et al. 2008), provide new opportunities to gain insights on diversity-invasibility relationships and underlying mechanisms. So far, only a few pioneering studies have combined functional, experimental, and modeling approach to investigate invasion mechanisms (Frankow-Lindberg et al. 2009e, Frankow-Lindberg 2012, Byun et al. 2013). Using controlled mesocosm experiments, the first study (Chapter 3) showed that functional

group identity and diversity of wetland plants determined biotic resistance to invasion by an exotic macrophyte, *P. australis*, suggesting priority effect and niche partitioning as primary resistance mechanism. However, scaling up to a large field experiment is necessary to address new questions about invasion dynamics using a variety of functional groups and levels of species diversity, as well as taking into account the diversity of natural invaders and the effect of heterogeneous environments on biotic interactions. This requires integrating different novel analytical approaches into a coherent framework to disentangle multiple interacting diversity effects in a much more complex environment than that of confined mesocosms.

We present the results of a large community assembly experiment that aims to determine mechanisms of species interactions underlying diversity effects on invasibility. The study site, a wetland basin, was under high propagule pressure particularly from *P. australis*, one of the most aggressive invasive plants in wetlands of North America, as well as from other naturally dispersed species. We applied various seed mixtures in experimental plots and measured abundance of naturally dispersed invaders over two years. We hypothesized that: (i) functional group identity (proportion of certain functional group in communities) would provide selective resistance to invasion by specific invaders; (ii) functional group diversity in communities (functional complementarity) would reduce overall invasion by multiple invaders; (iii) flooding (as

the main environmental heterogeneous factor in the study site) effect on community invasibility would be invader-specific. Given the experimental design, we built diversity-interaction models (Kirwan et al. 2009, Connolly et al. 2013) based on structural equations. Then, we used a model selection approach and multimodel inference (Johnson and Omland 2004) to identify the best mechanisms determining community invasibility. We showed that functionally diverse communities are more resistant to invasion and that the negative diversity-invasibility relationship is mainly driven by the interaction between certain sets of functional groups with mixed effects of both functional group diversity and identity. By embracing complex invasion dynamics and multiple drivers, this study brings new insights into invasion and community reassembly processes of significance to ongoing ecological changes.

5.3. Materials and methods

Study site

The experimental site is located in a wetland basin (about 3 km × 1 km) in Saint-Étienne-de-Beauharnois in southwestern Quebec, Canada (Appendix 5-1a). We chose this site because an introduced lineage of *P. australis* forms very dense monospecific populations in the wetland basin. Propagule pressure from the surrounding *P. australis* stands was estimated at circa 3,000 seeds m² using a seed trap (0.5 m × 0.5 m). Such a high level of propagule pressure makes this site ideal to measure and compare level of community invisibility as some invasion will always occur. Soil texture was clay and its organic matter content was 3.80 ± 0.24%. Soil nitrate (N-NO₃) content was 2.14 ± 0.51 mg Kg⁻¹. Soil ammonia (N-NH₄) content was 47.93 ± 12.33 mg Kg⁻¹ (for nine soil cores collected prior to experiment, Nutrient and Trace Element Analysis Laboratories, McGill University). During the first year of establishment, moist soil conditions were maintained with water levels being on average just below the surface and only 25% of plots showing flooded area (water level above surface). In the second year, all plots were at least partly flooded.

We first created a large bare ground area (about 30 m × 150 m) in the wetland basin to simulate the common practice of disturbing or clearing wetland vegetation cover following control or restoration. We setup 10 m buffer zones between main experimental

areas and surrounding *P. australis* stands to minimize edge effects and encroachment of experimental sites by rhizomes or stolons. We mowed *P. australis* stands in the plots and carefully cleared all debris using an excavator (Appendix 5-1b). Then, experimental sites were covered with black plastic sheets (® Solmax; membrane no.820; thickness: 0.5 mm) for a year mostly to exhaust rhizomes by depriving sprouts from light and growing space. The application of herbicide can be effective to control *P. australis* in wetlands but this was not an option as it is prohibited by law in our region. We wanted, in any case, to restrict our experiment to the use of ecological approach. We had to manually pull out very few shoots of *P. australis* from surviving rhizomes in the following year. In May 2010, the plastic sheets were removed in the areas assigned for 98 experimental plots (2 × 3 m²). We left the plastic cover (1 m) between plots to further isolate them.

Seed mixture treatments

To prepare seed mixtures, we first selected 35 herbaceous plants representing the regional species pool in wetlands, constrained by seed availability. All species are wetland plants (wetland indicator statuses: OBL, FACW, or FAC; USDA PLANTS database), and are native, except for *Lolium multiflorum*, which is introduced but naturalized in the region. Then, species were classified into emergent functional groups based on their dissimilarity for a set of functional traits. Functional traits considered are

(1) life history and dispersal: life longevity, clonality, seed mass, (2) resource use efficiency: specific leaf areas, relative growth rate, and leaf nitrogen content, (3) dominance and storage: canopy height, leaf dry matter content. These traits are related to the functional classification of wetland plants (Boutin and Keddy 1993), leaf-height-seed (LHS) plant ecology strategies (Westoby 1998), and belong to the common core of plant traits which are associated with dispersal, establishment, and persistence (Weiher et al. 1999). We also consulted with an expert in functional ecology (Dr. Bill Shipley, personal communication) to verify our trait selections. Functional trait information was obtained from TRY global database of plant traits (Kattge et al. 2011a). For numerical traits, we used the median value of several measurements of functional traits per each species to build a species-trait matrix. We used cluster analysis with Gower's dissimilarity coefficient (*hclust* and *gowdis* in R) for the classification of functional group (Figure 3-1). The resulting four functional groups differ mostly by plant life history and canopy height at maturity (Appendix 5-2a). FG1 are short annual plants. FG2 are biennial or short-lived perennial without rhizome. FG3 and FG4 are long-lived clonal perennial with rhizome. FG3 and FG4 differ mostly by canopy height at maturity (FG3: short; FG4: tall). Our plant functional group system can be compared with the Boutin and Keddy (1993)'s functional classification of wetland plants as indicated by shared species that belong to both systems. FG1 is approximately similar to obligate annual (ruderal), FG2 ~ facultative annual (ruderal) and reed (interstitial), FG3 ~ tussock and

clonal (interstitial), and FG4 ~ clonal dominant (matrix) (Dr. Paul Keddy, personal communication). Our system is also similar to Grime's CSR life history strategies: FG1~Ruderal, FG2~CSR, FG3~Stress tolerators, and FG4~Competitors (Appendix 5-2b).

Experimental design

We manipulated initial community composition by applying different species mixtures in terms of both taxonomic diversity and functional diversity. For species richness treatments, we drew 4, 8, and 16 species at random from the species pool of 35 wetland plants in addition to control (no seeds) for 7 times. The random draw is to minimize biased effect by certain species or functional group identity, often hidden in diversity treatments (Huston 1997). To create a variety of functional group composition, we drew 4 or 8 species, half of them from the functional group(s) of interest and the rest from the overall species pool at random 7 times. As a result of the species draw, overall ratios of FGs in mixtures were nearly balanced. A total of 98 species mixtures (14 treatments, replicated 7 times) was applied in a randomized complete block design (RCBD). Most seeds were purchased from seed suppliers (© Prairie Moon Nursery; © Shooting Start Native Seeds). We used a single-seed lot per species, which was harvested from an identified ecotype in natural habitat across North America. Seeds of wild *Typha sp.* were collected from a pond at the Montreal Botanical Garden in late fall

of 2009. Seed viability among wetland plants was standardized by applying pure live seeds rate (PLS = seed purity rate \times seed viability rate) per species. We stored all seeds at 4 °C for cold stratification until applied. In spring 2010, we sowed seed mixtures evenly into plots. Seeding density in a seed mixture was fixed at 2,000 pure live seeds m⁻², and all species were represented in equal proportions in a seed mixture. The sowing density is within the range of soil seedbank in natural or restored wetland (Galatowitsch and van der Valk 1996).

Field data sampling

We distinguished “sown species” (explanatory variable, applied as seed mixtures) from “unsown species” (response variable as a measure of community invasibility). The unsown species represented species not sown anywhere and therefore either true invader from outside the experimental system or species having survived and germinated from the seedbank (Frankow-Lindberg et al. 2009e, Frankow-Lindberg 2012). Fargione and Tilman (2005) define them as “non-experimental invaders”. It is reasonable to assume that the effect of seedbank species was evenly distributed among treatments thanks to our randomized complete block design. No matter whether seeds arrived from outside the system or, more rarely, germinated, from the seedbank, both contribute to propagule pressure to which sown communities are submitted.

Two growing seasons after initial sowing (in fall 2011), we measured the number of individual shoots (as plant density) and the plant cover (%) for each species within a plot. Plant cover (%) was estimated to the closest 0.5 % using reference frames representing 50%, 25%, 12.5%, 5%, and 1% of the total plot area. We also measured flooded area (%) in plot three times per each year and used the average of these measurements for analysis.

Data analysis

We analyzed data from the second year of experiment to quantify accumulated invasion by unsown species. Thus, we used absolute abundance of unsown species in a community to quantify community invasibility. As the main response variables, we used either (1) the sum of plant covers of all unsown species in a community (hereafter total unsown species) to take into account plant size effect among species or (2) the number of shoots of each major unsown species that invaded a community (species with frequency > 50 %: *Salix alba*, *Populus tremuloides* and *Phragmites australis*; Appendix 5-3). The former estimates overall community invasibility (as related to multiple invaders) and the latter estimates invader-specific community invasibility.

To test the effects of species or functional group richness of sown species on abundance of unsown species in a community (the classical hypothesis of diversity-

invasibility relationship), we used generalized linear mixed model (GLMM) with REML taking into account random block effect. We also included flooded area per plot (%) as a covariant in these analyses. We did not include an interaction term between flooding and diversity because it was not significant in preliminary test. Because functional group richness and species richness are highly correlated ($r=0.82$), we performed additional analysis to test the effect of functional group richness at a given interval of species richness (*coplot* and *panel.lm* in R).

We used diversity-interaction models based on structural equations (Kirwan et al. 2009, Connolly et al. 2013) to determine mechanisms underlying diversity-invasibility. We built six diversity-interaction models consisting of diversity-interaction terms, identity terms, and a covariant of flooding to test multiple hypotheses simultaneously. For details on model structure, equations and their biological assumptions, see Box 1. These sets of models represent almost every possible mechanism given the experimental design (Appendix 5-4). Based on findings of a previous study (Byun et al. 2013) that used the same functional classification system, our main assumption was that species identity effect of wetland plants on biotic resistance to invasion is determined by their functional group identity.

We used a model selection approach to disentangle complex dynamics of invasion processes. The model selection approach offers some important advantages compared to traditional null hypothesis tests (van Kleunen and Johnson 2007a). There is no restriction such as nesting models in hierarchical way unlike log-likelihood ratio method. Models can be also ranked (weighted), thereby providing a quantitative measure of evidence in favor of best model over a set of candidate models. We used Akaike's information criterion (AIC) and Akaike weight to compare several models' fit and parsimony simultaneously (Burnham et al. 2002, Johnson and Omland 2004). Use of AICc (second-order AIC) is recommended when sample size (n) is relatively small compared to the number of estimated parameters (K) ($n/K < 40$) (Burnham *et al.* 2002). We first selected the best model with smallest AICc. Then we calculated Akaike weights (w_i) using *AICcmodavg* packages in R. Akaike weights (w_i) can be viewed as the probability that model i is the best model given a set of model candidates (Johnson and Omland 2004). Because we found Akaike weights of the best model was less than 0.9 (i.e., evidence was not strong enough to support a single best model), we used model averaging as multimodel inference (*modavg* in R) to estimate important model parameters and test their significant effects. Model averaging makes multimodel inference based on weighted support from a set of alternative models (Prieur-Richard et al. 2000, Johnson and Omland 2004). The model parameters for model averaging were selected from good models ($\Delta \text{AICc} < 2$). In all analyses, the assumptions of normality of

residuals and homoscedasticity were checked, and response variables (abundance of unsown species) were natural-log-transformed to meet the assumption. We used R software (<http://www.r-project.org>) for all statistical analyses.

Box 1: Diversity-interaction models' structure, equations and assumptions

Diversity-interaction models estimate diversity effect based on pairwise species interactions (Kirwan *et al.* 2009). Where there are species *i* and *j* in a community, their diversity effect (DE) on ecosystem function (invasion resistance in our case) is as follows,

$$DE = \sum \delta_{ij}(P_i \cdot P_j)$$

where δ_{ij} is a coefficient to measure the strength of interaction between two species and their signs (\pm) represent whether their contribution is synergistic or antagonistic (Kirwan *et al.* 2009).

Model structure

$$Y = 1|\text{Block} + \text{Cov} + \text{DE} + \text{ID} + \varepsilon$$

Our diversity-interaction models consist of random block effect (**1|Block**), a covariate of flooding (**Flood**), diversity-interaction effect terms (**DE**), and selective identity effect

terms (ID). We constructed models by combining different types of DE and SE terms in factorial ways (3 DE × 2 ID =6 models; Appendix 5-4).

Diversity-interaction models

Model 1. Functional group identity and functional group interactions model

$$Y = 1|Block + Flood + \beta \cdot P_{FG1} + \beta \cdot P_{FG2} + \beta \cdot P_{FG3} + \beta \cdot P_{FG4} + \beta \cdot P_{FG1} + \delta \cdot P_{BFG12} + \delta \cdot P_{BFG13} + \delta \cdot P_{BFG14} + \delta \cdot P_{BFG23} + \delta \cdot P_{BFG24} + \delta \cdot P_{BFG34}$$

$$\text{Where } P_{FG1} = \sum P_i \text{ (} i \in FG1\text{)}; P_{BFG12} = \sum P_i \cdot P_j \text{ (} i \in FG1; j \in FG2\text{)}. \quad \text{eqn 1}$$

The coefficient β of P_{FG1} represents identity effect of FG1 to contribute to the selection effect; the coefficient δ of P_{BFG12} represents interactions between FG1 and FG2 to contribute to the complementarity effect. Assumption: Both selection effect (FG identity) and complementarity diversity effect (pairwise interactions of functional groups) determine community invasibility.

Model 2. Functional group identity and species evenness model

$$Y = 1|Block + Flood + \beta \cdot P_{FG1} + \beta \cdot P_{FG2} + \beta \cdot P_{FG3} + \beta \cdot P_{FG4} + \beta \cdot P_{FG1} + \delta_{av} \sum P_i \cdot P_j$$

$$\text{Where } P_{FG1} = \sum P_i \text{ (} i \in FG1\text{)}; \delta_{av} \sum P_i \cdot P_j \quad \text{eqn 2}$$

The coefficient β of P_{FG1} represents identity effect of FG1 to contribute to the selection effect; the coefficient δ_{av} represents species evenness effect on average.

Assumption: In addition to selection effect (FG identity), species interactions equally contributes to diversity effect. (Compared to model 1, species interactions are even regardless of functional group composition).

Model 3. Functional group identity model

$$Y = 1|Block + Flood + \beta \cdot P_{FG1} + \beta \cdot P_{FG2} + \beta \cdot P_{FG3} + \beta \cdot P_{FG4} + \beta \cdot P_{FG1}$$

$$\text{Where } P_{FG1} = \sum P_i (i \in FG1); \delta_{av} \sum P_i \cdot P_j \quad \text{eqn 3}$$

The coefficient β_{FG1} represents identity effect of FG1. Assumption: Selection effect of FG identity determine invasibility (Compared to model 1 and 2, there is no diversity effect (null species interactions) on invasion).

Model 4. Functional group interactions model

$$Y = 1|Block + Flood + \delta \cdot P_{BFG12} + \delta \cdot P_{BFG13} + \delta \cdot P_{BFG14} + \delta \cdot P_{BFG23} + \delta \cdot P_{BFG24} + \delta \cdot P_{BFG34}$$

$$\text{Where } P_{BFG12} = \sum P_i \cdot P_j (i \in FG1; j \in FG2). \quad \text{eqn 4}$$

The coefficient δ of P_{BFG12} represents interactions between FG1 and FG2 to contribute to the complementarity diversity effect. Assumption: Complementarity diversity effect (pair wise functional group interactions) solely determine community invasibility. There is no selection effect of functional group identity.

Model 5. Averaged species interaction model (evenness model)

$$Y = 1|Block + Flood + \delta_{av} \sum P_i \cdot P_j \quad \text{eqn 5}$$

, where the coefficient δ_{av} represents species evenness effect on average.

Assumption: pairwise species interaction equally contributes to diversity effect.

Model 6. Null species interaction model

$$Y = 1|Block + Flood \quad \text{eqn 6}$$

Assumption: there is no effect of seed mixture treatments on invasion. Abiotic constraint solely determine invasion.

5.4. Results

Community assembly and major invaders

For sown species, annuals (FG1) were dominant over perennials in the first year of the experiment (2010), but biennials or perennials became dominant in the following year (Appendix 5-5). Among unsown species, *P. australis* invaded 94% of plots while most other unsown species invaded less than 10% of plots in the first year. In the following year, the major invading unsown species were *P. australis* (exotic species; 97% of plots), *Salix alba* (exotic; 88% of plots), and *Populus tremuloides* (native; 87% of plots) while the other unsown species invaded less than 40% of plots (Appendix 5-3).

Diversity-invasibility

Abundance of total unsown species (the invaders in a plot) significantly decreased in logarithm manner with increasing species richness of sown species (the restored community) in 2011 ($t=-2.66$; $p=0.015$; Figure 5-1). Regarding particular invaders, both *P. australis* ($t=-3.09$; $p=0.005$) and *S. alba* ($t=-3.89$; $p=0.001$) decreased with increasing sown species richness, but the trend was not significant for *P. tremuloides* ($t=-1.34$; $p=0.194$). Abundance of total unsown species also significantly decreased with increasing functional group richness (FGR) of sown species ($t=-4.45$; $p<0.001$) in 2011 (Figure 5-2). Again, the effect of FGR was significant for *P. australis* ($t=-2.70$; $p=0.008$) and *S. alba* ($t=-6.17$; $p<0.001$), but marginal for *P. tremuloides* ($t=-1.66$; $p=0.100$). When we tested the same FGR effect in given species richness intervals, the effect of FGR was stronger and significant in communities with less than 6 species, compared to communities with more than 6 species (Appendix 5-6). Flooding significantly decreased the abundance of total unsown species ($t=-4.07$; $p<0.001$), as well as of *P. tremuloides* ($t=-4.45$; $p<0.001$) and *S. alba* ($t=-0.20$; $p=0.041$), but increased abundance of *P. australis* ($t=3.09$; $p=0.002$).

Diversity-interaction model

Comparison of model based on Akaike criterion information are shown in Table 5-1. For total unsown species and *S. alba*, it was best described by model 4 (functional group

interactions model) which had the lowest AICc and highest Akaike weight (0.62 and 0.72, respectively). For *P. australis* and *P. tremuloides*, model 3 (functional group identity model) showed the highest Akaike weight (0.51 and 0.33), while model 4 (functional group interactions model) remained among the best models as well (Δ AICc < 2, Akaike weight: 0.33 and 0.26).

In model averaging for multimodel inference, significant decrease in the abundance of total unsown species was best described by interactions between certain pairs of functional groups (FG1×FG2 and FG3×FG4; Table 5-2). These interactions also explained reduced invasion by specific invaders, although the significant group interaction terms selected varied with invaders (e.g., FG1×FG2 against *P. australis*; FG1×FG3 against *S. alba*; Table 5.2). Functional group identity terms (FG1 and FG4) selectively influenced invasion of specific invaders (FG1 against *P. australis*, FG4 for *P. tremuloides*, null selection effect for *S. alba*). Flooding as a model covariant generally reduced wetland plant community invasibility, but responses varied with invaders, with *P. australis* showing better flooding tolerance than *S. alba* or *P. tremuloides*.

5.5. Discussion

We expected diversity in a community to be inversely related to invasibility (Tilman 1997, Symstad 2000, Fargione and Tilman 2005, Pokorny et al. 2005, Frankow-

Lindberg et al.), but our experiment reveals inherently complex and dynamic diversity-invasibility relationships even at fine scale. It delivers important messages for understanding the ecological mechanisms involved: (i) interactions between certain pairs of functional groups in a community mainly drive the diversity effect on community invasibility (ii) dominance of certain functional group in a community selectively reduces invasion success of specific invaders (*P. australis* and *P. tremuloides*).

The negative diversity-invasibility relationship in this study suggests that, as species/functional groups are being added, niches are getting saturated and resource uses overlap in communities. Niche saturation, however, does not necessarily lead to complete depletion of available resources and thereby will not completely repel invasion even in undisturbed communities (Tilman 1997), especially at high propagule pressure. Instead, biotic resistance can constrain the abundance, and consequently the impact of invaders (Levine et al. 2004).

Both complementarity diversity effect and selection effect contribute to invasion resistance (Fargione and Tilman 2005, Frankow-Lindberg et al. 2009e). This study shows that their relative contribution depends on the diversity of invaders. Previous studies have shown that selection effect of certain species (van Ruijven et al. 2003, Emery and Gross 2007) or functional groups (Fargione et al. 2003, Sheley and James

2010) can influence invasion resistance when examined against a particular invader. Our results also indicate substantial selection effect of certain functional group for specific invader (e.g., FG1 for *P. australis*; FG4 for *P. tremuloides*). Complementarity diversity effect, on the other hand, had much stronger influence on overall community invasibility to multiple invaders. Our findings support (Funk et al. 2008)'s hypothesis that functionally redundant communities may be more resistant against certain invader at low diversity, but communities with functional complementarity will be resistant against multiple invaders at high diversity. It does not support Fox's assembly rule, however, since the functional group most similar to *P. australis* (FG4) was not the most resistant. Meta-analysis of synthetic-assemblage experiments suggests similar functional groups may be resistant to forb invaders, supporting limiting similarity, but not to grass invaders (Price and Pärtel 2013). These invader-specific responses further complicate diversity-invasibility relationships and make the search for generalized pattern difficult.

Significant interactions between certain pairs of functional groups (FG1×FG2 and FG3×FG4) show that functional group composition is as important as functional diversity (Tilman 1997) against a notion that all kinds of functional groups equally matter (Pokorny et al. 2005, Rinella et al. 2007). More importantly, our findings suggest life history trade-off (FG1×FG2), partitioning of canopy layers (FG3×FG4), and the both (FG1×FG4) as fundamental mechanisms underlying diversity effect. Annuals (FG1)

establish earlier than perennials and therefore pre-empt available niches (Mwangi et al. 2007). Such priority effect can be particularly important to interfere with early perennial invaders like *P. australis* (Byun et al. 2013). Successional transition of species with different life history insures the maintenance of biotic resistance over time by filling temporal gaps in phenological niche (Wolkovich and Cleland 2010, Wilsey et al. 2011). Inclusion of additional functional groups could provide further insurance against other invaders over time, but that would need to be verified through long-term investigation.

A significant interaction of FG3×FG4 suggests a different mechanism underlying diversity effect; they are similar in terms of life history and clonality but differ mostly in canopy height. Coexistence of FG3 and FG4, therefore, results in the partitioning of the canopy layer and more efficient light interception. Less light reaches the soil surface, modifying microhabitat conditions for establishment (Lindig-Cisneros and Zedler 2002c). Evidence of the efficiency of resource partitioning in diverse communities has also been proposed in terms of soil nitrogen uptake (Tilman 1997, Booth et al. 2003, Frankow-Lindberg 2012). Efficient resource uptakes result in increased biomass of the resident community, one of the best indicators for potentially strong biotic resistance to invasion (Lulow 2006, Rinella et al. 2007).

Both *in situ* heterogeneous environments and selective propagule pressures from metacommunities determine the functional type of invaders at community level. Invader-specific responses to flooding regime in our study show that environmental gradients first filter out invaders. Flooding inhibited invasion by *P. tremuloides* (FACU) and likely other upland species, but allowed invasion by *P. australis* (OBL/FACW in wetland indicator status). The study site was seasonally flooded at shallow water level after the first year of invasion by *P. australis* and thereby *P. australis* seedlings were able to survive because their flooding tolerance increases with age and they have phenotypic plasticity to adjust to shallow water level, but not to prolonged submergence (Mauchamp et al. 2001). Fluctuating environmental conditions in time and space often offer windows of opportunities for seedling establishment, facilitating invasion.

Diversity-invasibility patterns have been reported to vary from regional to local scale, but diversity effect can also become weaker in the field compared to those detected in the controlled environment of fine-scale experiments because of environmental heterogeneity (Balvanera et al. 2006). For instance, complementarity diversity effect was stronger than selection effect against invasion by *P. australis* in mesocosm experiments (Byun et al. 2013), while both were equally important in the field for this species.

Propagule pressure is one of the major drivers for invasion success (Lockwood et al. 2005), and it sometimes overwhelms biotic resistance to invasion and even to some extent the filtering effect of abiotic conditions (Holle and Simberloff 2005). In our study, most experimental communities were invaded by *P. australis* to different degrees under strong propagule pressure from surrounding stands. Like *P. australis*, the two other major invaders in our system produce large amounts of wind-dispersed seeds that facilitate long-distance dispersal. Among other unsown species, however, great variation in the percentage of invaded plots (Appendix 5-3) could partly reflect differences in colonization pressure from nearby meta-communities (Lockwood et al. 2009).

In the context of multiple species introductions and rapid environmental changes, one can expect reorganization of species within potentially novel communities. Our findings suggest that functionally diverse native communities, with the partitioning of resources in time and space, have greater chance to resist invasion. Maximizing functional group interactions within resident communities may serve as an insurance to ward off invasion by multiple invaders if the goal is to maintain or restore native biodiversity at a location. Community dynamics, however, can be quite complex even at fine scale and the relative contribution of functional diversity and functional composition vary with the

species involved, making it sometimes difficult to predict specific diversity-invasibility outcomes without a detailed knowledge of the ecology of the species involved.

The main invader in our system was introduced *P. australis*, a species of high concern in wetlands of North America. At locations under high propagule pressure from specific aggressive invaders, such as *P. australis* or species with similar functional characteristics, restoring native communities taking into account the role of biotic resistance can be an innovative ecological management strategy to limit invasion. This has yet to be widely addressed or applied (Kettenring et al. 2011), however, and would require a good knowledge of species interaction mechanisms. In the particular case of introduced *P. australis* in wetlands, our results suggest that functional group composition may become more significant than diversity in assembling invasion-resistant communities. For instance, the order of influence of functional groups and group interactions from standard coefficient values suggests that the effect of FG1 > FG1-FG2 > FG1-FG4 > FG3-FG4 in limiting invasion by *P. australis*. If seed mixtures are applied to restored sites within the critical window of establishment opportunity, short annual plants should be included (>50%), ideally combined with non-clonal biennial (~25%) and/or tall clonal perennial (~25%). Species and location-specific assessment may be necessary though for information about best practices to emerge. In any case, maximizing functional interactions seems key to success.

By proposing an integrated analytical framework and new evidence of functional interacting mechanisms in a realistic setting that takes into account multiple factors, our study has far-reaching implications for community theory and practical applications beyond the case of particular invaders. It is an important step in reconciling the often-conflicting perspectives on diversity-invasibility and the relative role of multiple ecological drivers. By embracing complexity, it offers directions to help formulate and test predictions about the nature and the relative importance of functional mechanisms determining invasion success or biotic resistance in variable environments, whether the invaders are exotic or not. We believe that the new insights that it provides for invasion and community ecology are of relevance to a rapidly changing world.

5.6. Tables

Table 5-1: Comparison of diversity-interaction models based on model fit

Models	k	All invaders		<i>P. australis</i>		<i>S. alba</i>		<i>P. tremuloides</i>	
		Δ AICc	w_i	Δ AICc	w_i	Δ AICc	w_i	Δ AICc	w_i
Model 4*	10	0.00	0.62	0.85	0.33	0.00	0.72	0.44	0.26
Model 3	8	2.43	0.18	0.00	0.51	8.46	0.01	0.00	0.33
Model 1	14	3.16	0.13	8.35	8.35	1.96	0.27	3.36	0.06
Model 2	9	4.51	0.07	2.42	0.15	10.97	0.00	2.44	0.10
Model 5	5	13.04	13.04	14.71	0.00	23.00	0.00	1.58	0.15
Model 6	4	19.54	19.54	18.88	0.00	32.92	0.00	2.35	0.10

Model 1: Functional group identity and functional group interactions model, Model 2: Functional group identity and species evenness model, Model 3: Functional group identity model, Model 4: Functional group interactions model, Model 5: Species evenness model, Model 6: Null species interaction model

Δ AICc = AICc - minimum AICc among models. Lower Δ AICc indicates better model fit. Good models (Δ AICc <2) are in bold. Akaike weight (w_i) = an estimated probability that model i is the best model, given 6 models.

§Number of model parameters. *The best model for all invaders and *S. alba* and good model (Δ AICc <2) for *P.*

australis and *P. tremuloides*. ¶Null model includes background terms, such as model intercept, random block effect, and a covariant of flooding %.

Table 5-2: Model parameters estimation based on the model averaging. Terms are ordered in descendent estimates (less β_{std} value means more resistant to invasion).

Best Models	All invaders		<i>Phragmites australis</i>		<i>Salix alba</i>		<i>Populus tremuloides</i>	
	terms	$\beta_{std} \dagger$	terms	β_{std}	terms	β_{std}	Terms	β_{std}
Model 4	FG3×FG4	-0.32 ± 0.09*	FG1×FG2	-0.43 ± 0.12*	FG1×FG3	-0.33 ± 0.10*	Flooding	-0.37 ± 0.08*
	FG1×FG2	-0.30 ± 0.09*	Flooding	0.35 ± 0.10*	FG1×FG2	-0.30 ± 0.10*	FG2×FG4	-0.23 ± 0.09*
	Flooding	-0.26 ± 0.07*	FG1×FG4	-0.33 ± 0.12*	FG3×FG4	-0.28 ± 0.09*	FG3×FG4	-0.22 ± 0.11*
	FG1×FG4	-0.16 ± 0.08*	FG3×FG4	-0.31 ± 0.11*	Flooding	-0.13 ± 0.06*	FG2×FG3	0.11 ± 0.10
	FG2×FG3	-0.08 ± 0.09	FG2×FG4	0.18 ± 0.11	FG1×FG4	-0.12 ± 0.10	FG1×FG3	-0.02 ± 0.10
	FG1×FG3	-0.05 ± 0.08	FG2×FG3	-0.16 ± 0.11	FG2×FG3	-0.11 ± 0.10	FG1×FG4	0.01 ± 0.10
	FG2×FG4	0.01 ± 0.08	FG1×FG3	-0.13 ± 0.11	FG2×FG4	0.05 ± 0.08	FG1×FG2	-0.00 ± 0.10
Model 3	FG1	-0.41 ± 0.10*	FG1	-0.60 ± 0.14*	FG1	-0.50 ± 0.10*	FG4	-0.31 ± 0.10*
	FG4	-0.28 ± 0.09*	FG4	-0.27 ± 0.13	FG4	-0.25 ± 0.09*	FG2	-0.18 ± 0.12
	FG2	-0.22 ± 0.12	FG3	-0.23 ± 0.15	FG2	-0.23 ± 0.11*	FG3	-0.02 ± 0.11
	FG3	-0.21 ± 0.11	FG2	-0.15 ± 0.16	FG3	-0.22 ± 0.10*	FG1	0.07 ± 0.10

† β_{std} Standardized coefficient ± standard error *Significant model parameters ($P < 0.05$) in bold

5.7. Figures

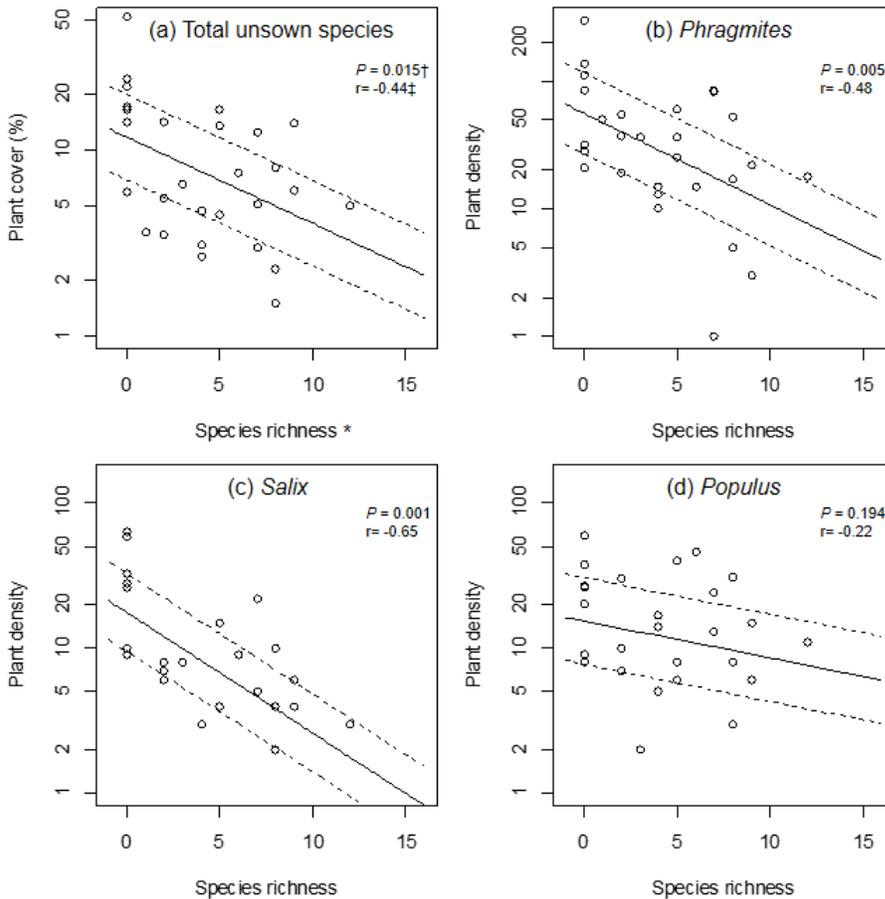


Figure 5-1: The effect of sown species richness on abundance of unsown species: (a) all invaders (sum of unsown species), (b) *Phragmites australis*, (c) *Salix alba*, and (d) *Populus tremuloides* in 2011.

The Y-axis was log-transformed. Solid line represents simple linear regression fit.

Dotted lines represent 95% confidence interval. *Sown species richness represents the number of species that established from seed mixtures. †significance of generalized linear mixed model including terms of species richness, covariant (flooding), and random block. ‡Pearson's correlation coefficient

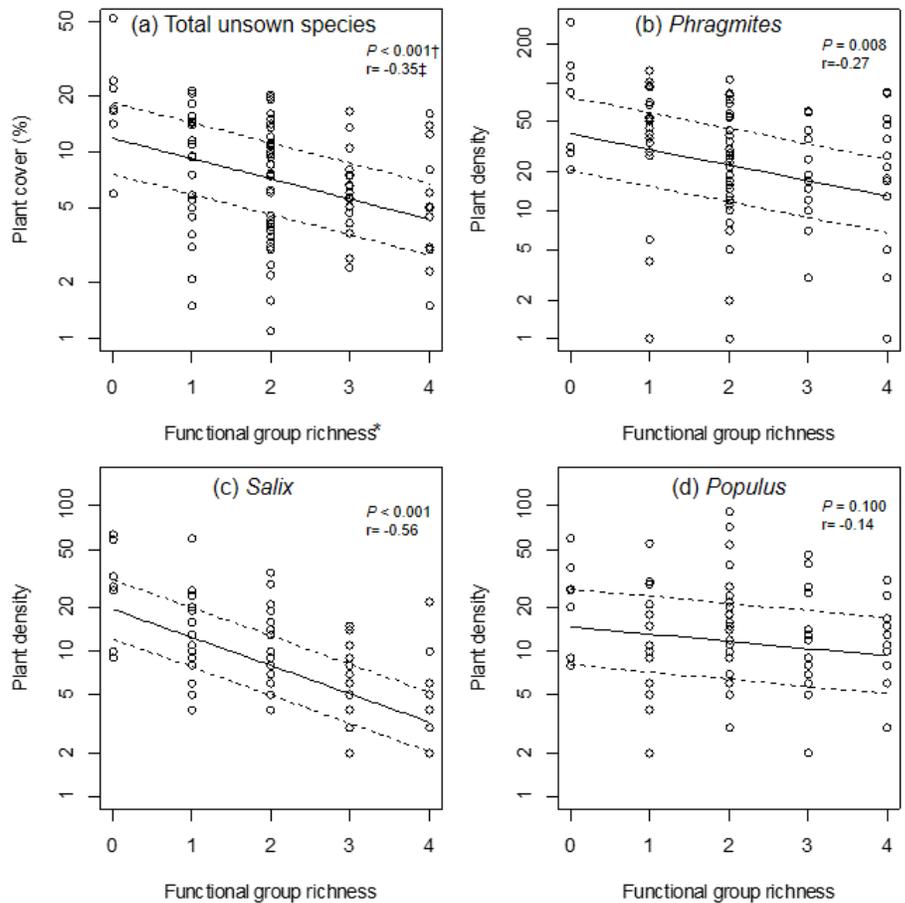


Figure 5-2: The effect of functional group richness of restored plant communities on abundance of unsown species: (a) total unsown species, (b) *Phragmites australis*, (c) *Salix alba*, and (d) *Populus tremuloides* in 2011.

The Y-axis was log-transformed. *Number of functional groups that established from seed mixtures. Solid line represents simple linear regression fit. Dotted lines represent 95% confidence interval. †Significance of generalized linear mixed model including terms of FG richness, covariant (flooding), and block. ‡Pearson's correlation coefficient

Chapter 6 Discussion and Conclusion

In this chapter, I synthesize the main findings of Chapter 3, 4, and 5 by revisiting each research question and hypothesis. Then, I discuss how these findings contribute to advance knowledge in the study field. I also address implications for ecological application in invasive plant management. Finally, I briefly make suggestions for future research directions.

6.1. Revisiting research questions and hypothesis

My research focuses on determinants of biotic resistance in plant community assembly, with relevance for species invasion and ecological restoration. In the first study (Chapter 3), I delved into a research question, “what kind of species (individual) will resist most to invasion?”, using *P. australis* invasion on wetland soil inside pots as model system for my study. I found sufficient evidence supporting the hypothesis that (1) functional group identity is a good predictor of biotic resistance to *P. australis* (in other words, biotic resistance of one species is significantly related to its functional group identity while biotic resistance would be redundant within each functional group). The most resistant group of species has distinct functional characteristics (e.g. short life span and height, fast growth rate) which provide species with fitness advantages (e.g. priority effect), mainly in the first year, a critical window of invasion opportunity. However, there was

only limited evidence to support limiting similarity or fox's assembly rule (i.e., a community with the functional group that is similar to an invader is the most resistant). In addition, mixtures of four species were more resistant to invasion, compared to the average performance of monocultures, supporting the (2) diversity-resistance hypothesis. Analytic results indicate that the diversity effect is possibly driven by "complementarity" diversity effect. By applying a functional group framework, this study provides general plant characteristics offering strong biotic resistance. The case study was with *P. australis*, but the findings may well apply to other species as well. However, this first study was done under homogenous conditions and with a limited number of species combinations (only eight mixtures). Therefore, in the second study (Chapter 4), I assessed "how biotic resistance interacts with abiotic constraints and propagule pressure". I hypothesized that biotic resistance to *P. australis* will be modulated by how each wetland plant species responds to an abiotic constraint (flooding) while the direct effect of this constraint will also affect *P. australis* seedling establishment. I also hypothesized that there is a threshold in the propagule pressure's impact on invasion by *P. australis* and it can be controlled by increasing sowing density of wetland plants. To test these hypotheses, I measured biotic resistance in two different abiotic conditions (moist versus flooded) and modified sowing densities (five levels for *P. australis* and three levels for wetland plants mixtures) in two separate pot experiments. Results from analytic modeling (i.e., applying structural equation modeling to experimental data)

suggest that abiotic constraint and biotic resistance can synergistically or antagonistically work in controlling invasion depending on anaerobic tolerance of wetland species. For instance, impact of flooding on species resistance was negative for *Lolium multiflorum*, positive for *Typha latifolia*, and neutral for mixtures. The strong and stable biotic resistance of mixtures supports the insurance hypothesis among various mechanisms underlying biodiversity-ecosystem functions. These experiments provide unique evidence that there are significant interactions between biotic resistance and abiotic constraints as well as propagule pressure. This finding suggests that entangling complex invasion processes is only possible through synthetic approach to address invasions.

In the third study (Chapter 5), I attempted to expand the context of ecological resistance by conducting a large-scale experiment in a wetland basin. The main research questions were to determine which plant communities restored from applied seed mixtures most restrain recruitment of new species under field conditions, and to quantify the relative importance of different inhibitors of invasion, either for one specific or for multiple invaders. I hypothesized that both species diversity and functional group composition in the seed mixtures can be good predictors of the biotic resistance of the restored plant communities to new species recruitment, while their relative importance may differ according to specific invaders. It shows, for the first time, that interactions

between certain pairs of functional groups mainly drive the diversity effect underlying biotic resistance while certain functional groups selectively restrain a specific invader. This result implies that interactions between functional groups are key mechanisms generating a diversity effect. By embracing complex invasion processes and multiple drivers, this study not only advances our comprehension of early community assembly and response to invasion, but also proposes a useful analytical framework that we hope will inspire future investigations and experimentations in the field of community and invasion ecology.

6.2. Implications for management of invasive plants

In addition to contributing to general restoration principles, my research also has more specific implications on how to manage the introduced lineage of *P. australis*, which is one of the most aggressive invasive plants in North American wetlands. In order to restore vegetation cover in a recently disturbed wetland while preventing invasion of *P. australis* by seeds, based on my results, I recommend the use of seeding mixes with specific plant species combinations, as follows:

- **Functional group composition:** the seeding mix for wetland restoration should include > 50% of ruderal plants (short life span and height, high growth rate; FG1), ideally combined with interstitial plants of intermediate life span and height, relatively short

and shallow roots, but high growth rate (FG2 ~25%) and/or long-lived, tall clonal dominant plants (FG4 ~25%).

- **Species selection:** Excellent species candidates for wetland restoration, in the different functional group category are, among ruderals (FG1): *Bidens connate*, *Bidens cernua*, *Eleocharis obtusa*, *Lolium multiflorum*; among interstitials (FG2): *Mimulus ringens*, *Carex hystericina*; and among clonal dominant (FG4): *Leersia oryzoides*, *Scheoenoplectus tabernaemontani* and *Typha latifolia*. Non-clonal, perennial matrix species with deep root (FG3) may not be necessary in preventing *P. australis* invasion.

- **Number of species:** 3-4 species

More than 4 species may be desirable for other restoration purposes (for instance increase site diversity), but my results show it does not bring significant additional benefits in terms of resistance to invasion to *Phragmites australis*. Instead, a certain functional group (FG1) and its interactions with other functional groups is much more important for strong biotic resistance. For resistance to *P. australis* alone, I would rather recommend to invest in increasing sowing density of wetland plants rather than increasing species diversity, given limited resources.

- **Seed density:** 3,000 seeds·m⁻² or more to control over 80% of low propagule pressure (1,000 seeds·m⁻²). This sowing density is within the range of common restoration practices. There is a threshold effect in the relationship between sowing

density and biotic resistance. For instance, if one puts more than 10,000 seeds·m⁻², it may not be cost-effective. Effective sowing density depends on *in situ* propagule pressure from *P. australis*. For instance, sowing 2,000 seeds·m⁻² or more can control more than 70% of propagule pressure (1,000 seeds ·m⁻²) of *P. australis*. If propagule pressure cannot be estimated, one may need to apply more seeds to ensure strong biotic resistance as the site gets closer to the source (mature stands of *P. australis*). For instance, distance to seed source (within a circle of 1-10 km radius) can be a strong indicator of propagule pressure which can be inversely proportional to the square of the distance between source and sink.

- **Early intervention:** To protect conservation area from possible invasion by undesirable species like *P. australis*, the rules of thumb- early detection and fast response – can be applied. The earlier the restoration intervention, the more likely it will be preventing *P. australis* invasion. During wetland restoration, sowing seed mixtures or planting seedlings early should be mandatory to keep restoration site from possible invasion.
- **Environment:** If a site experiences intermittent flooding during a year, inclusion of *Typha* sp. (cattail) or other flood-tolerant species will be necessary. According to the result from the second study (Chapter 4), *Typha* sp. can actively adapt to flooding conditions and thus flooding can further increase their biotic resistance. Prolonged

flooding may inhibit or delay emergence of restored wetland plants (with less flood-tolerance) as well as of *P. australis*.

6.3. Suggestions for future study directions and closing remarks

Nowadays, there is much interest for improving our ability to understand and predict how communities will be reshuffled through the introduction of exotic species (in a context of new invasion pathways) or migration of native ones from warmer places (in a context of global changes). This study proposes a useful analytical framework that we hope will inspire future ecological research. Important messages for guidelines include (but are not limited to): (1) functional trait can be a powerful analytic tool to understand species interaction mechanisms or diversity effect on resistance; (2) plant functional groups/strategies can be good predictors for community assembly and invasibility; (3) synthetic approach (e.g. addressing multiple factors in a single study simultaneously) is a key to entangle apparent complexity and find hidden ecological principles. I believe my study can be an important step toward predicting invasion risk and impact as well as designing native community assembly for invasive plant management. My study provides new guiding principles for community invasibility based on ecological theory; it has great potential for the development of new invasion hypothesis of functional group (e.g. functional group composition in plant communities determines biotic resistance). I propose to test this new invasion hypothesis against different invasive plants, or in

different environment or contexts to make further generalization. It may bring out significant insights on invasion ecology as well as community ecology, and increase our capability to cope with new invaders in a rapidly changing world.

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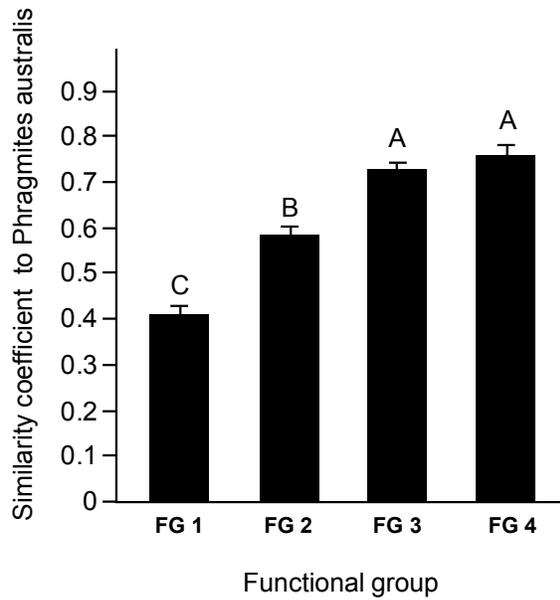
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Appendices

Appendices to Chapter 3

Appendix 3-1: Average similarity coefficient of wetland plants to *P. australis* in each functional group. Error bar shows standard error of mean. Functional groups connected by same letter are not significantly different from each other.



Appendix 3-2: Functional trait characteristic of each functional group

Values of numerical functional traits represent mean \pm standard error of mean.

Functional trait (unit)	Functional group			
	FG 1	FG 2	FG 3	FG 4
Life longevity	annual	perennial	perennial	perennial
Growth form¶	single crown or bunch	single crown, single stem, bunch, stoloniferous	rhizomatous	rhizomatous
Seed dry mass* (mg 1000 seeds ⁻¹)	1.83 \pm 0.61	0.19 \pm 0.25	0.59 \pm 0.20	5.25 \pm 4.70
Specific leaf area (mm ² mg ⁻¹)	27.0 \pm 4.3	22.0 \pm 3.1	23.0 \pm 1.6	15.6 \pm 4.1
Leaf nitrogen content (mg g ⁻¹)	19.6 \pm 1.28	20.1 \pm 1.78	17.8 \pm 1.61	19.7 \pm 3.24
Relative growth rate* (g g ⁻¹ day ⁻¹)	0.26 \pm 0.01	0.27 \pm 0.02	0.20 \pm 0.01	0.20 \pm 0.01
Leaf dry matter content (g g ⁻¹)	0.19 \pm 0.02	0.23 \pm 0.01	0.24 \pm 0.01	0.27 \pm 0.04
Plant height at maturity* (m)	0.86 \pm 0.14	1.02 \pm 0.07	0.87 \pm 0.08	2.47 \pm 0.20

*Numerical functional traits were significantly different (*F* test; *P* < 0.05) among FGs.

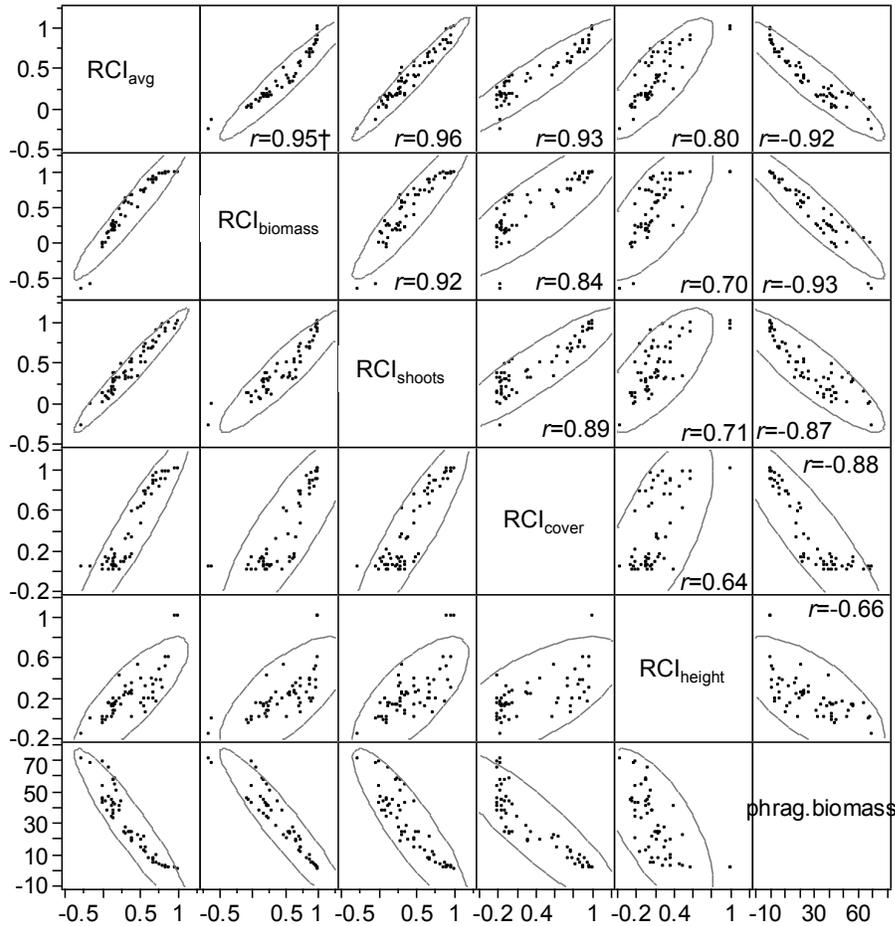
¶Growth form definition follow USDA's PLANTS database definition (single crown: A herbaceous plant that develops one persistent base; single stem: plant development by the production of one stem; bunch: plant development by intravaginal tillering at or near the soil surface without production of rhizomes or stolons; stoloniferous: plant development by the production of stolons which give rise to vegetative spread; rhizomatous: plant development by the production of rhizomes which give rise to vegetative spread).

Appendix 3-3: Overview on experiment (photo taken in 2009 summer)



Appendix 3-4: Correlations among different response variables (RCI_{avg} , $RCI_{number\ of\ shoot}$, $RCI_{biomass}$, RCI_{height} , $RCI_{plant\ cover}$, and biomass of *P. australis*) in the experiments.

†the r values represent Pearson correlation coefficient.



Appendix 3-5: Partitioning diversity effect equation

Original equation about partitioning diversity effect (Loreau and Hector 2001) was modified by replacing response variable, yield with RCI_{avg} (relative competitive effect on *P. australis*), as follows.

$$\Delta Y = Y_o + Y_e = \sum_i RY_{o,i}M_i - \sum_i RY_{e,i}M_i = \sum_i \Delta RY_i M_i = N\overline{\Delta RYM} + N\text{cov}(\Delta RY_i, M_i)$$

Where,

ΔY = net diversity effect in term of relative competitive effect on *P. australis* (RCI_{avg}) in a mixture

Y_o = observed competitive effect in the mixture

Y_e = expected competitive effect in the mixture

$RY_{o,i} = Y_{o,i} / M_i$ = observed relative competitive effect of species *i* in the mixture

M_i = competitive effect of species *i* in the monoculture

$Y_{o,i} = P_i \times Y_o$

P_i = Relative cover of species *i* in the mixture (Note: it was originally relative *y*)

$RY_{e,i}$ = proportion of species *i* in the mixture

$\Delta RY_i = RY_{o,i} - RY_{e,i}$ = deviation from expected relative competitive effect of species *i* in the mixture.

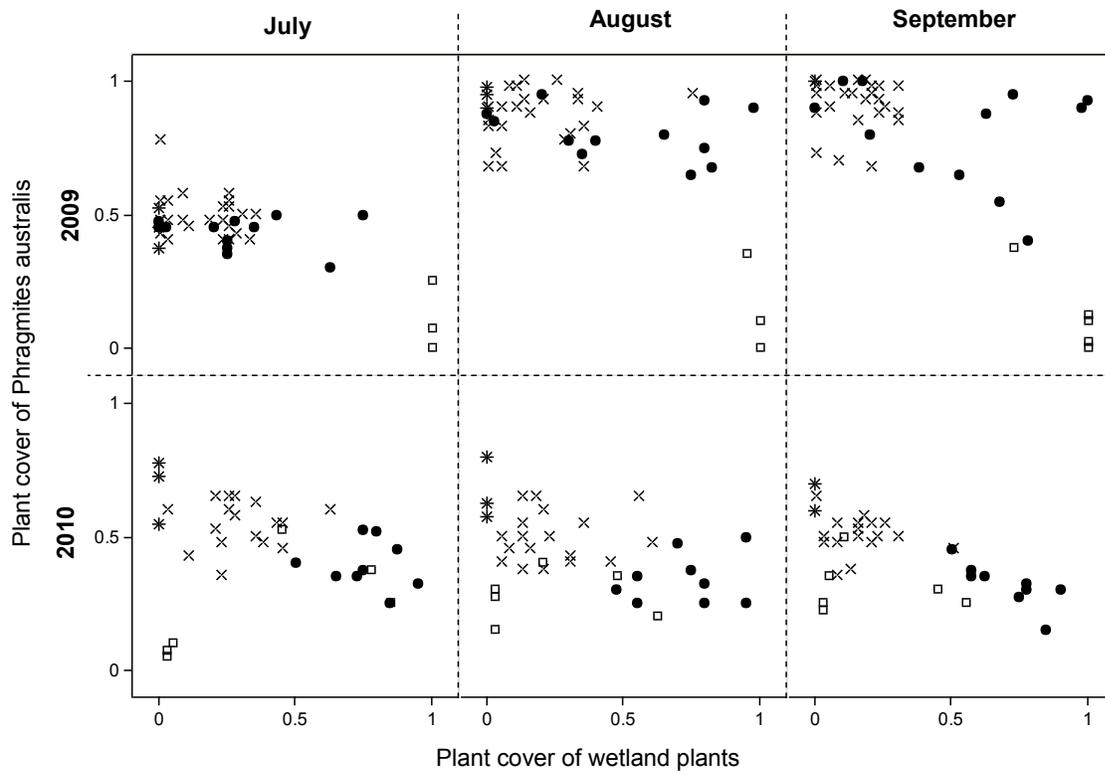
In this equation, $N\overline{\Delta RCM}$ represents the complementarity effect, and $N\text{cov}(\Delta RY_i, M_i)$ represents selection effect in terms of competitive effect.

This equation is based on the assumption that invasion resistance of each species in mixture is proportional to “plant cover” of the species in the mixture ($C_{o,i} = P_i \times C_o$). Because there was significant and positive relationship between plant cover of resident species and RCI_{avg} in simple linear regression model ($F_{1,55} = 71.96$; $P < 0.001$), the assumption was reasonable (Dr. Michel Loreau, personal communication).

Appendix 3-6: Results of statistical analysis on biomass of *P. australis* in monoculture experiments.

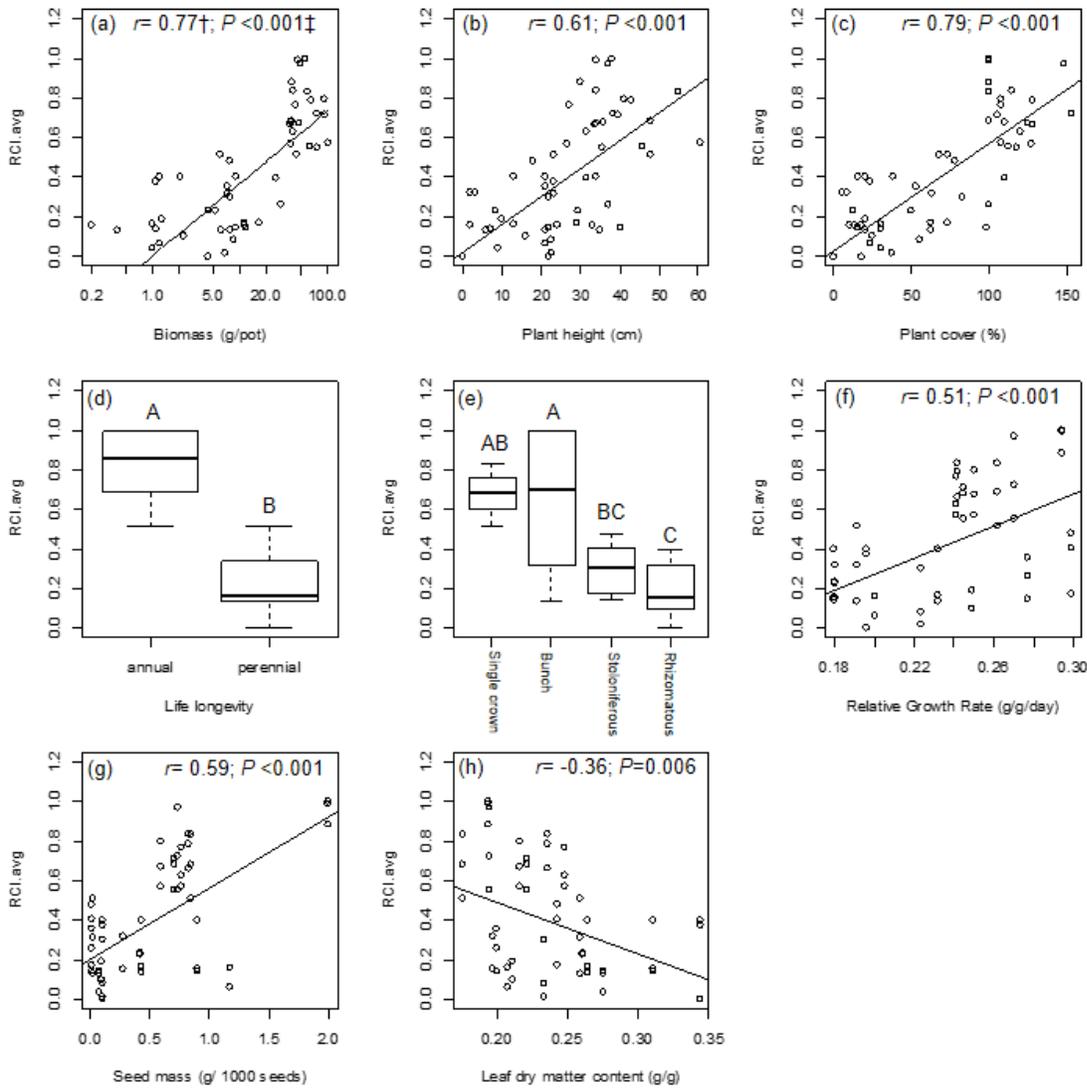
In 2009 for the first experiment, biomass of *P. australis* was significantly different among three FGs ($F_{2,20} = 25.21$, $P < 0.001$), but it was not significantly different within each FG ($F_{8,20} = 2.00$, $P = 0.098$). In 2010 for the first experiment, biomass of *P. australis* was significantly different among three FGs ($F_{2,20} = 28.14$, $P < 0.001$), but it was not significantly different within each FG ($F_{8,20} = 0.96$, $P = 0.492$). In 2011 for the second experiment, biomass of *P. australis* was significantly different among four FGs ($F_{3,48} = 8.96$, $P < 0.001$), but it was not significantly different within each FG ($F_{21,48} = 1.73$, $P = 0.059$).

Appendix 3-7: Change in plant cover of wetland plants and *P. australis* from 2009 to 2010



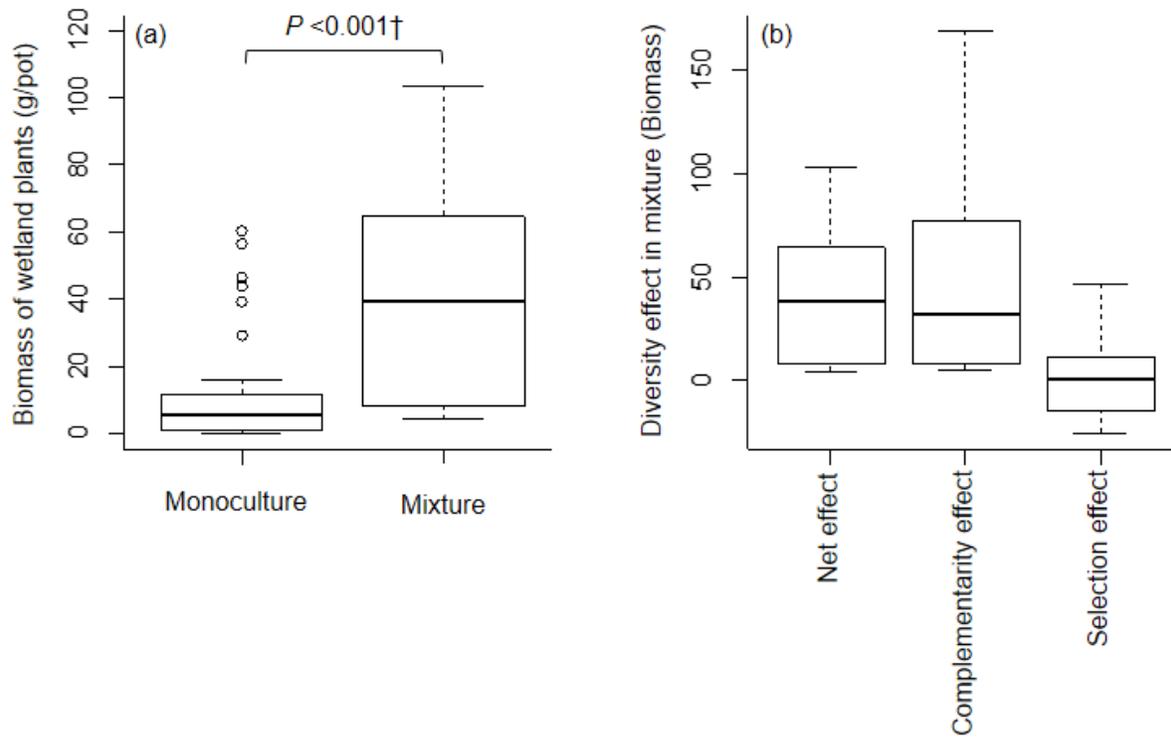
Legend * Control □ FG 1 ● FG 2 × FG 3

Appendix 3-8: Relationship between plant traits and biotic resistance (RCI_{avg}) in the first experiment. Performance trait (from experiment): (a) biomass, (b) plant height, and (c) plant cover; Functional traits (from TRY trait database): (d) life longevity, (e) growth form, (f) RGR, (g) seed mass, and (h) LDMC.



Solid line represents linear regression fit (log-scale was used in case of biomass). Means connected by same letter are not significantly different from each other in ANOVA test (life longevity: $F_{1,29}=63.83$; $P < 0.001$; growth form: $F_{3,27}=10.81$; $P < 0.001$). Only functional traits that have significant relationship with RCI_{avg} are shown. † values represent Pearson correlation coefficient. ‡ values represent t test result on slope in linear regression analysis.

Appendix 3-9: Partitioning diversity effect based on biomass of resident species in mixture experiment. †Contrast test result



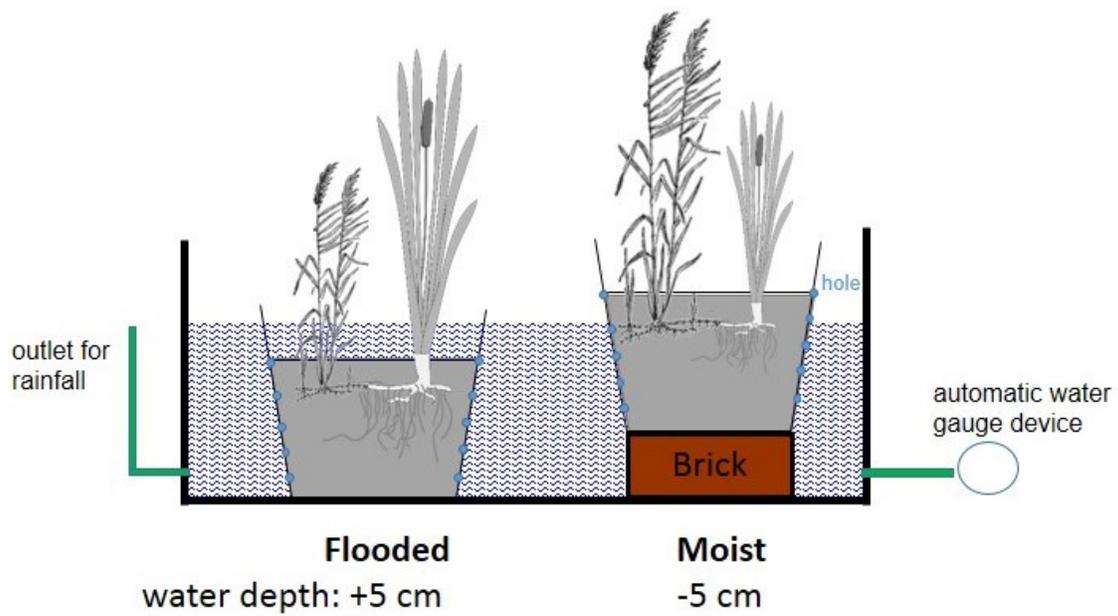
Appendix 3-10: Summary of diversity-interaction model results.

Diversity interaction models (model term description)	K	AIC††	Model terms ($P < 0.05$)		
			model term	P	Estimate
Model 1 (species identity effect)	11	-14.43	β_{Lolium}	<0.001	1.190
			β_{Bidens}	<0.001	0.712
			$\beta_{Mimulus}$	0.012	0.396
			$\beta_{Scirpus}$	0.0474	0.308
			$\beta_{Calamagrostis}$	0.0475	0.311

Model 2			β_{FG1}	<0.001	0.971
(functional group identity effect):	3	-16.44	β_{FG2}	0.012	0.339
Model 3			β_{FG1}	<0.001	0.895
(functional group identity effect and	4	-26.16	β_{FG2}	0.023	0.281
average species interaction)			δ_{av}	0.001	0.436
Model 4			β_{FG1}	<0.001	0.817
(functional group identity effect	9	-43.12	β_{FG2}	0.004	0.308
and species interaction within and			$\delta_{FG1-FG3}$	<0.001	2.219
between functional group)					
Model 5			β_{FG1}	<0.001	0.832
(functional group identity effect and	58	-41.26	β_{FG2}	<0.001	0.319
separate species interactions)			$\delta_{Lolium-Panicum}$	0.001	5.222
			$\delta_{Lolium-Mimulus}$	0.001	5.047
			$\delta_{Lolium-Scirpus}$	0.021	2.011
Model 6			β_{FG1}	<0.001	0.811
(functional group identity effect	6	-44.46	β_{FG2}	0.006	0.295
and species interaction between			$\delta_{FG1-FG3}$	<0.001	2.098
functional group)					

¶ Akaike information criterion

Appendices to Chapter 4

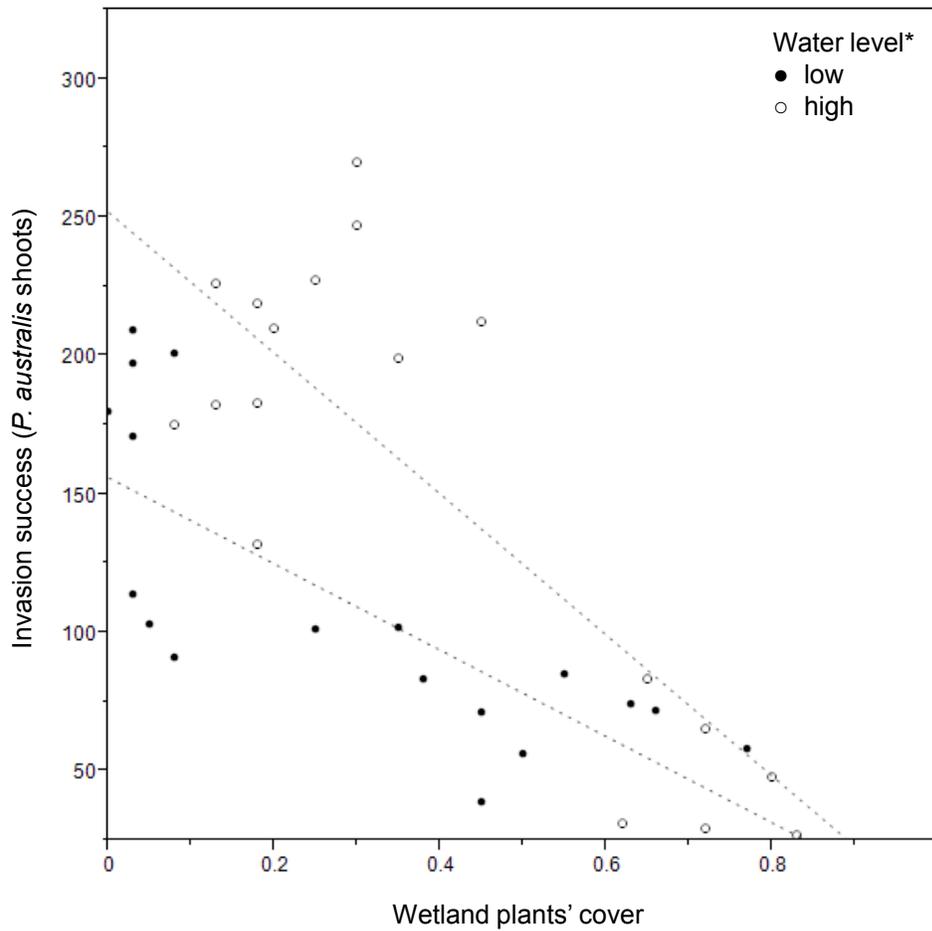


Appendix 4-1 Experimental design: treatments of water levels (moist vs. flooded).

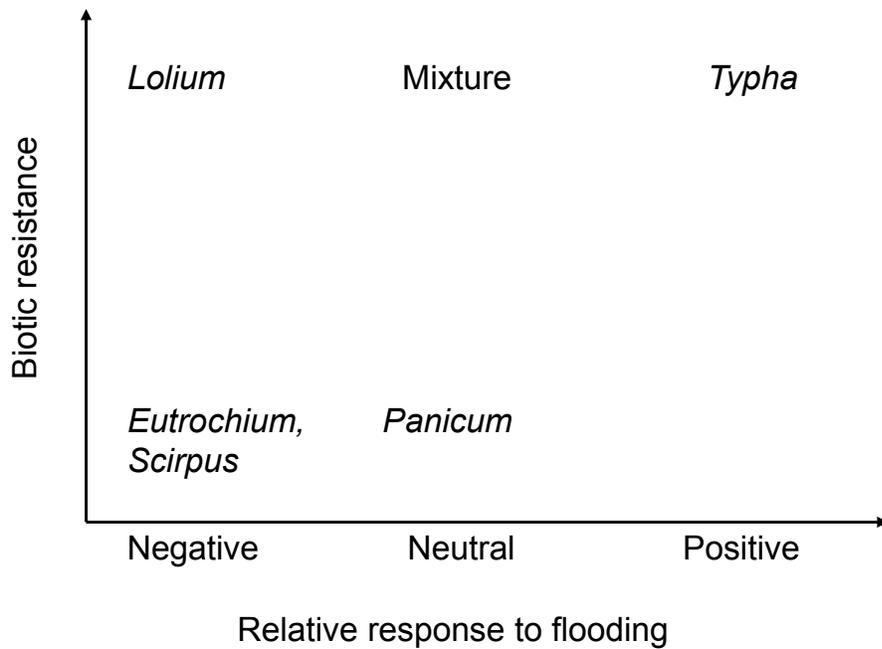
Appendix 4-2 Information about experimental plants

Species	Anaerobic tolerance ¹		Life form ²	Wetland indicator status (and origin) ³
	At maturity	At seedling	(Raunkiaer)	
<i>Lolium multiflorum</i>	Low	Low	Therophyte	FACU (I)
<i>Eutrochium maculatum</i>	Low	Low	Hemicryptophyte	FACW (N)
<i>Scirpus cyperinus</i>	Intermediate	Intermediate	Hemicryptophyte	FACW (N)
<i>Panicum virgatum</i>	Intermediate	Intermediate	Cryptophytes (Geophytes)	FACW (N)
<i>Typha latifolia</i>	High	High	Cryptophytes (Hydrophyte)	OBL (N)
<i>Phragmites australis</i>	High	Low	Cryptophytes (Geophytes)	FACW (I)

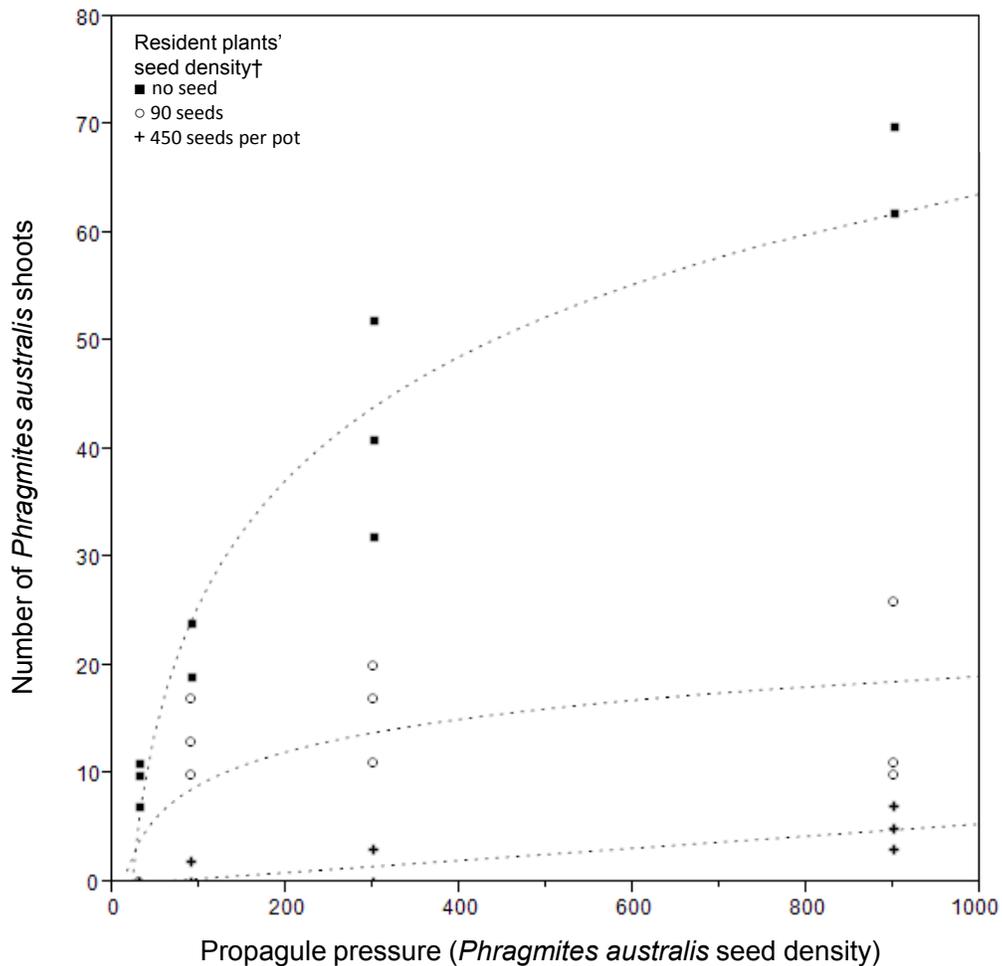
¹References for anaerobic tolerance of each species are as follow. *L. multiflorum*: Carey (1995), *E. maculatum*: Kercher and Zedler (2004), *S. Cyperinus*: Fraser and Karnezis (2005), *P. virgatum*: Barney et al. (2009), *T. latifolia*: Kercher and Zedler (2004), *P. australis*: Weisner et al. (1993), Mauchamp et al. (2001). Most information at mature stage was obtained from PLANTS database (USDA NRCS 2009) except *E. maculatum*, which was obtained from Illinois Native Plant Guide (NRCS 2008). ²Scoggan (1978), Flora of Canada. ³USDA PLANTS database (<http://plants.usda.gov>). (FAC)ultative (U)pland or (W)etland species; (OBL)igate; (N)ative; (I)troduced.



Appendix 4-3 Relationship between wetland plant cover and *P. australis* invasion success, compared by *water levels (●: low, 5cm belowground ○: high, 5cm aboveground). Dotted lines represent simple linear regression at each water level



Appendix 4-4 Characterisation of resident species in terms of flood tolerance and biotic resistance to *Phragmites australis*. Anticlockwise from top-right (1) flood-adaptive and invasion-resistant (*Typha latifolia*), (2) flood-tolerant and invasion-resistant (6-species mixture), (3) flood-intolerant and invasion-resistant (*Lolium multiflorum*), (4) flood-intolerant and invasion-susceptible (*Eutrochium maculatum* and *Scirpus cyperinus*), and (5) flood-tolerant and invasion-susceptible (*Panicum virgatum*). There were no flood-adaptive and invasion-susceptible (bottom-right) species in this study.



Appendix 4-5a Bivariate plot of the relationship between propagule pressure and invasion success of *P. australis*, given seed density of resident species (a mixture of *Lolium multiflorum* and *Typha latifolia*). Dotted lines represent simple regression model fits, given seed density of resident plants (no seed: linear-log; 90 seeds: linear-log; 450 seeds: linear). Model fit comparison using AICc determined the best model (Online Resource 5b).

Appendix 4-5b Model comparison about the shape of the relationship between propagule pressure and *P. australis* invasion, depending on the seed density of resident species.

Regression model fit	AICc (Akaike weight)		
	Other plants' seed density		
	No seed	90 seeds	450 seeds
Linear	92.01(0.02)	89.42 (0.08)	47.8(0.93)*^c
linear-log	84.31(0.98)*^a	84.47 (0.92)*^b	53.11(0.07)

*Best model(s) with the lowest AICc

^aLinear-log model equation: $y = -49.58 + 16.39 \cdot \log(x)$; $R^2_{\text{adjust}} = 0.92$

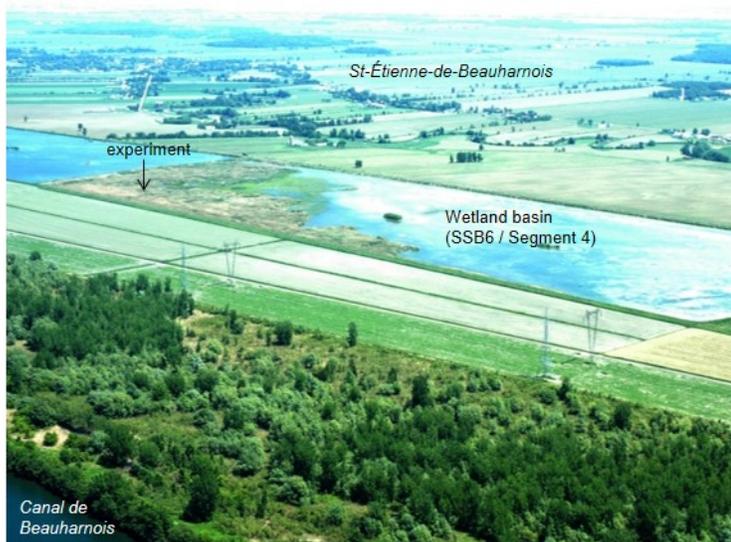
^bLinear-log model equation: $y = -10.89 + 4.33 \cdot \log(x)$; $R^2_{\text{adjust}} = 0.44$

^cLinear model equation: $y = -0.18 + 0.0056 \cdot x$; $R^2_{\text{adjust}} = 0.68$

Appendices to Chapter 5

Appendix 5-1 Study site location, procedures of construction of field experiment

Appendix 5-1a Overview of study site (a) regional map of study site, (b) experimental site in a wetland basin.



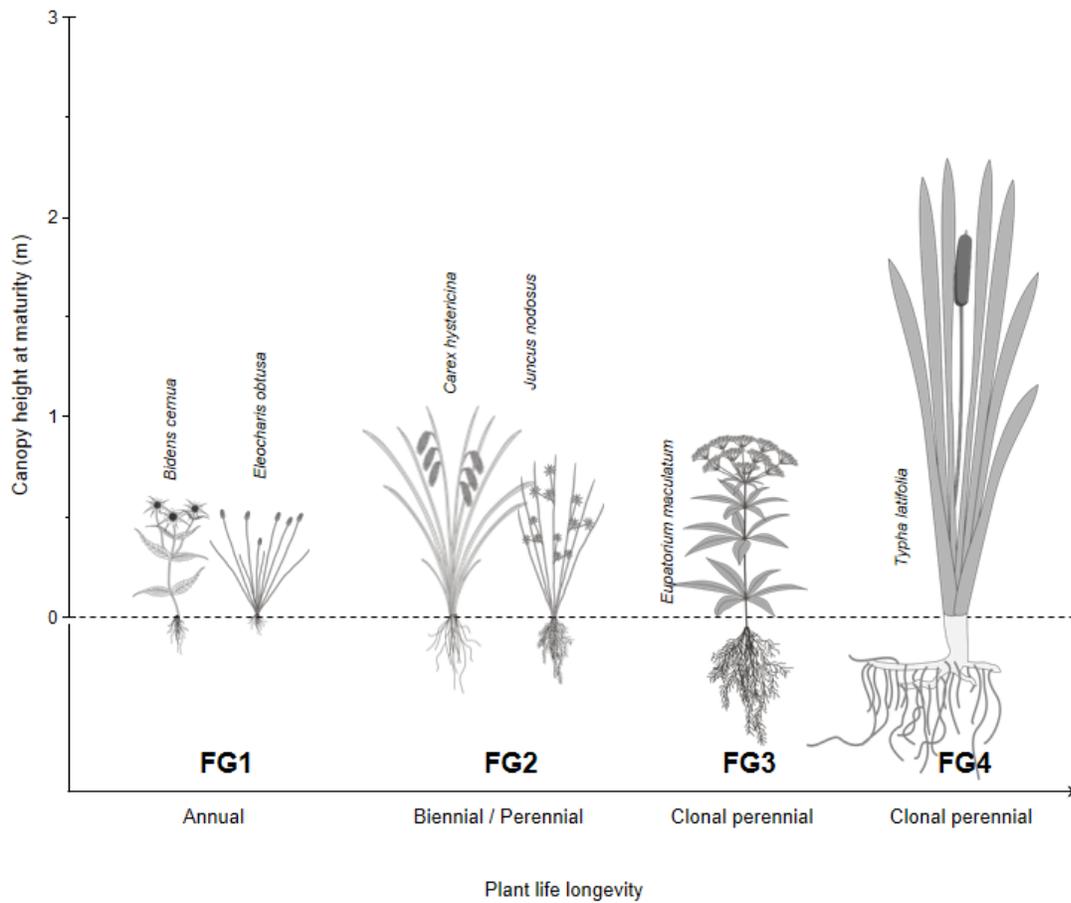
The study site is located in a wetland basin (45°14'33.51"N, 73°57'29.90" W), Saint-Étienne-de-Beauharnois, Quebec, Canada. The site was previously used as a sediment basin from 1960 to 1979 during construction of the Beauharnois canal. After 1979, the wetland became drier and an introduced lineage of *Phragmites australis* invaded (personal communication with André Michaud, Ducks Unlimited in Canada).

Appendix 5-1b Preparing the experimental site (a) original *Phragmites australis* stands in 2008, (b) mowing, (c) covering black plastic for solarisation in 2009 summer, (d) treatment plots to apply seed mixtures in 2010 spring

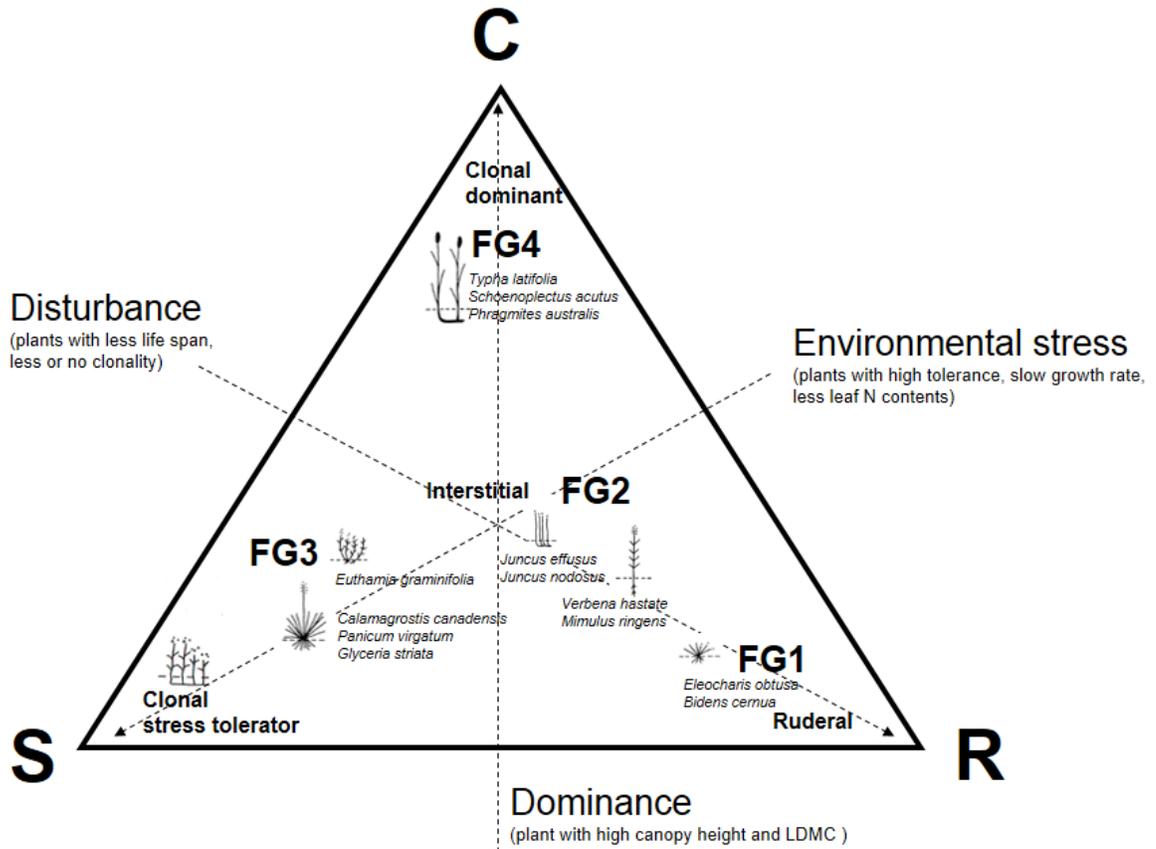


Appendix 5-2 Functional classification of wetland plants into emergent functional groups based on functional trait dissimilarity.

Appendix 5-2a Major characteristic of each functional group in our system



Appendix 5-2b Comparison with other systems, including functional classification of wetland plants (Boutin 1993) and Grime' CSR life history strategies (Grime 1977)



Appendix 5-3 List of unsown species

Species*	Origin*	Impact†	Life span	Wetland Status	% plots Invaded
<i>Phragmites australis</i>	exotic	invasive	perennial	FACW	96.9%
<i>Populus tremuloides</i> §	native	none	perennial	FACU	87.8%
<i>Salix alba</i> §	exotic	none	perennial	FACW	86.7%
<i>Epilobium hirsutum</i>	exotic	none	perennial	FACW	38.8%
<i>Cyperus strigosus</i>	native	none	perennial	FACW	35.7%
<i>Lycopus europaeus</i>	exotic	invasive	perennial	OBL	29.6%
<i>Lythrum salicaria</i>	exotic	invasive	perennial	FACW	26.5%
<i>Taraxacum officinale</i>	exotic	none	perennial	UPL,FACW	17.3%
<i>Persicaria lapathifolia</i>	exotic	none	annual	FAC	7.1%
<i>Symphotrichum lanceolatum</i>	native	none	perennial	OBL	5.1%
<i>Galium tinctorium</i>	native	none	perennial	FACW	3.1%
<i>Solidago canadensis</i>	native	none	perennial	FACU	2.0%
<i>Impatiens capensis</i>	native	none	annual	FACW	2.0%
<i>Echinochloa crus-galli</i>	exotic	none	annual	FACU	2.0%
<i>Agrostis gigantea</i>	exotic	none	perennial	FAC	2.0%
<i>Ranunculus sceleratus</i>	native	none	annual	OBL	1.0%
<i>Phalaris arundinacea</i>	exotic	invasive	perennial	FACW	1.0%
<i>Galium palustre</i>	native	none	perennial	OBL	1.0%
<i>Panicum capillare</i>	native	none	annual	FACU	1.0%
<i>Solidago rugosa</i>	native	none	perennial	FAC	0.0%

*Species nomenclature and origin follow the Vascular Plants of Canada (VASCAN) database. Invasiveness in study region.

‡Wetland indicator status (data source: USDA PLANTS Database)

Appendix 5-4 Configuration of diversity-interaction models (1: include; 0= exclude).

Models	Flood	BFG	Sl _{av}	FG ID
Model 1	1	1	0	1
Model 2	1	0	1	1
Model 3	1	0	0	1
Model 4	1	1	0	0
Model 5	1	0	1	0
Model 6	1	0	0	0

Flood: covariance, BFG: interaction between functional groups, Sl_{av}: average species interaction (species evenness), and FG ID: functional group identity.

Appendix 5-5 Overview of experiment community reassembly

First year of experiment



Second year



Third year



Appendix 5-6 The effect of functional group richness in seed mixture on abundance of unsown species, given sown species richness intervals: (a) 0 to 2 species, (b) 3 to 4 species, (c) 5 species, and (d) 6 to 12 species. The conditional plots were drawn using *panel.lm* and *coplot* function in R. The interval was automatically determined by the *coplot* with the option of no overlapping (assigning similar number of points into each interval). Solid line represents simple linear regression fit. *number of species established from seed mixture. †*t* test results of the regression. ‡Pearson's correlation coefficient.

