

ECOLOGICAL AND ECONOMIC IMPACTS OF AN INVASIVE PLANT SPECIES

A Thesis

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by

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ABSTRACT

Although invasive species are defined by U.S. law as species that cause environmental or economic harm, we have a limited understanding of each concept. In my thesis, I use both ecological and economic methods to explore the impacts of non-native plants. In Chapter 1, I report the results of a two experiments in which I tested whether plant-derived compounds have an impact on larval amphibian performance, and whether this effect is predictable by plant native/non-native status. I find that tannins, saponins, and leachate from certain plant populations impact amphibian survival, rate of metamorphosis, and size—traits linked to adult fitness. In Chapter 2, I report my findings from a survey of 285 public and private land managers from across the United States. In total, managers spend at least \$4.6 million on *Phragmites australis* (common reed) control. Over 90% of these organizations have applied herbicide in the past five years, treating a total of 83,000 wetland hectares with 28,000–20,000,000 L of herbicide product. Despite this high expenditure of resources and chemicals, organizations report that they rarely accomplish management objectives. In Chapter 3, I use conjoint analysis, a method of non-market valuation, to describe the impact of invasive plants in terms of management trade-offs rather than dollar value. It is my hope that a more synthetic understanding of invasive plant management will lead to more economically and ecologically sustainable land stewardship.

BIOGRAPHICAL SKETCH

Laura grew up in a white wooden house built by her grandfather in Manville, Rhode Island. During that time she wanted to become a pediatrician, UN speaker, astronaut, and chef (in that order). At 18 she began her undergraduate studies at Brown University in Providence, Rhode Island. In 2005 she participated in the Organization for Tropical Studies program in Costa Rica. Walking through humid rainforests and damp cloud forests, she discovered her passion for ecology. She graduated from Brown with honors in 2006, having focused on ecology, physics, and history (B.S. Biophysics).

After graduating, Laura spent a year working at the John Innes Centre in the labs of Drs. Johanna Schmitt (Brown University) and Caroline Dean (JIC). She spent her days counting tiny leaves of *Arabidopsis thaliana* in the drizzling English rain, studying the genetic mechanisms behind flowering time. She learned a lot from the field experience, and made close friends during her time in Norwich.

Interested in both ecology and conservation, Laura began a M.S./Ph.D. program at Cornell University in the Department of Natural Resources in fall of 2007. Laura is advised by Dr. Bernd Blossey. She will be continuing in a Ph.D. program, researching the environmental history and practice of ecological management. She currently lives in Ellis Hollow, NY, with her partner Zach. When not thesis-ing, she plays the fiddle, writes non-fiction and fiction, and learns new crafts.

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TABLE OF CONTENTS

Biographical sketch.....	iii
Acknowledgements.....	iv
Table of contents.....	v
List of Figures.....	vi
List of Tables.....	vii
Preface.....	viii
CHAPTER ONE: PLANT SECONDARY COMPOUNDS IMPACT THE PERFORMANCE OF LARVAL AMPHIBIANS.....	1
<i>Abstract</i>	1
<i>Introduction</i>	1
<i>Methods</i>	5
<i>Results</i>	10
<i>Discussion</i>	24
<i>References</i>	28
CHAPTER TWO: THE MONETARY AND CHEMICAL COSTS OF INVASIVE PLANT MANAGEMENT.....	37
<i>Abstract</i>	37
<i>Introduction</i>	37
<i>Methods</i>	40
<i>Results</i>	42
<i>Discussion</i>	52
<i>Appendix</i>	57
<i>References</i>	66
CHAPTER THREE: ECONOMIC IMPACT OF NON-NATIVE PLANTS IN TERMS OF TRADE-OFFS	75
<i>Abstract</i>	75
<i>Introduction</i>	75
<i>Methods</i>	79
<i>Results</i>	82
<i>Discussion</i>	86
<i>References</i>	88

LIST OF FIGURES

Figure 1.1. Final <i>L. palustris</i> and <i>A. maculatum</i> survival by treatment.....	14
Figure 1.2. Final <i>L. palustris</i> SVL by treatment.....	15
Figure 1.3. Survival of <i>A. maculatum</i> in <i>Phragmites</i> leachate over time.....	20
Figure 1.4. Final <i>A. maculatum</i> SVL and stage by <i>Phragmites</i> origin.....	21
Figure 1.5. Box plot of peak areas for unidentified compound.....	22
Figure 1.6. Examples of HP-LC peak area output.....	23
Figure 2.1. <i>Phragmites australis</i> invasion and management.....	43
Figure 3.1. Hypothetical impacts of invasion on Total Economic Value.....	77

LIST OF TABLES

<i>Table 1.1.</i> Locations of <i>Phragmites</i> litter collection.....	8
<i>Table 1.2</i> Experiment 1 model parameters.....	12
<i>Table 1.3.</i> Performance of <i>A. maculatum</i> and <i>L. palustris</i> by treatment.....	13
<i>Table 1.4</i> Experiment 2 model parameters.....	17
<i>Table 1.5.</i> Probability of <i>A. maculatum</i> survival in <i>Phragmites</i> leachate.....	18
<i>Table 1.6.</i> Performance of <i>A. maculatum</i> by <i>Phragmites</i> population.....	19
<i>Table 2.1.</i> Reasons for controlling non-native <i>Phragmites</i>	46
<i>Table 2.2.</i> Ratings of <i>Phragmites</i> management success.....	49
<i>Table 2.3.</i> Constraints on <i>Phragmites</i> management: actively managed.....	50
<i>Table 2.4.</i> Constraints on <i>Phragmites</i> management: not actively managed.....	51
<i>Table 3.1.</i> An example land attribute choice set.....	81
<i>Table 3.2.</i> Summary of respondent information.....	83
<i>Table 3.3.</i> Multinomial logit model estimates.....	85
<i>Table 3.4.</i> Marginal rate of substitution by type of organization.....	86

PREFACE

In my masters thesis (and onward towards my Ph.D.) I address one fundamental question: how can we approach land management with ecological relationships in mind? The following three chapters fall somewhere in-between plant ecology, animal ecology, conservation biology, sociology, resource economics, ecological economics, or economic ecology. I am intentionally blurring disciplinary borders in order to tackle the idea of ecological management.

There are currently more than 4,300 naturalized non-native species in the United States. Public and private conservation organizations actively manage a subset of these species, reacting to a doomsday scenario that has been portrayed by “best available science.” The general mantra has become “all invasive species are bad,” or as I heard at a recent FWS manager’s workshop, “the only good invasive is a dead invasive.” Recent findings in and outside of our lab, my own work (Chapter 1), and my rejection of the idea of static biotic communities, make me question the all-invaders-must-die approach. My findings on how much herbicide is being sprayed in wetlands (Chapter 2) add to my critique. I prefer a land management approach that is holistic (Chapter 3), one that judges management success by the state of the post-managed ecosystem rather than removal of the invader.

In my Ph.D. dissertation, I plan to explore the history of land management in the United States, connecting the past to my present-day critiques of conservation. My interest in land management emerges from my masters thesis, conversations in my lab and the department, and my general love of all things controversial.

CHAPTER 1

PLANT SECONDARY COMPOUNDS IMPACT THE PERFORMANCE OF LARVAL AMPHIBIANS

Abstract

Amphibians develop in a world that is structured by living and senescent plant material—plants provide shelter from predators, create microclimates, and are a main source of material in aquatic food-webs. The chemical composition of this plant material is known to indirectly influence amphibian performance through its role in litter decomposition; more recently, researchers have suggested that plant-derived compounds may also directly affect larval amphibian physiology. In order to test this hypothesis, we reared *Ambystoma maculatum* and *Lithobates palustris* larvae in set concentrations of purified tannin and saponin, as well as in leachate from various native and non-native *Phragmites australis* populations. Tannins, saponins, and some but not all *P. australis* leachates significantly decreased larval survival, developmental stage, and size of larvae—variables linked to adult fitness. Amphibian performance is best predicted by concentration of phytochemicals, not the native/non-native status of *P. australis* litter—suggesting that plant traits, not plant origin, best predict amphibian performance.

Introduction

Larval amphibians are captives of their surroundings. Occupying the littoral habitats of ponds and lakes, larvae develop in an environment that is determined partially by maternal choice and partially by chance (Bernardo 1996, Alford 1999). Traits of this environment influence timing of metamorphosis, a highly plastic

response that is directly related to adult fitness. Multiple abiotic and biotic factors have been linked with the timing and rate of metamorphosis, including hydroperiod, competition, predation, disease, food availability, temperature, and water chemistry (e.g. Rudolf and Rodel 2007, Gervasi 2007, Cohen et al. 2009). Plant species that grow and senesce in amphibian environments influence a number of these factors, including food availability (Findlay and Arsuffi 1989, Taylor et al. 1989, Driebe and Whitham 2000, Tuchman et al. 2002, Tuchman et al. 2003, Maerz Blossey and Nuzzo 2005, Cohen 2009), light and temperature regimes (Skelly et al. 2002, Halverson et al. 2003), and shelter from predators (Babbitt and Jordan 1996, Kopp et al. 2006). Perhaps the best-studied plant-amphibian interaction is the link between plant macronutrient stoichiometry, decomposition rates, and the aquatic food web (Cornelissen et al. 2004, Parsons et al. 2004, Schweitzer et al. 2004, Cebrian and Lartigue 2004, Moore et al. 2004, Rier et al. 2005, Schiesari 2006, Rubbo et al. 2008, Williams et al. 2008, Cohen 2009). More recently, researchers have considered whether plant-derived secondary compounds influence amphibian performance through their role in decomposition processes (Horner et al. 1988) or through direct physiological effects (Maerz et al. 2005, Brown et al. 2006).

Compounds that are derived from live or senescent plant material are known to impact a number of aquatic organisms. Two classes of compounds are particularly well-studied: tannins (polyphenols) and saponins (amphipathic glycosides). Tannins are known to inhibit digestion (Rosenthal and Janzen 1979), cause sub-lethal to lethal gill lesions in fish (Temmink et al. 1989), and bind with multiple proteins (Suberkropp et al 1976). Saponins can act as feeding repellents for insects (Herlt et al. 2002) and shrimp (Chen et al. 1996); they can also swell gill lamella and interlamellar epithelia (Roy et al. 1986, Roy and Munshi 1989), lyse blood cells (Tang 1961, Terazaki et al. 1980, Minsalan and Chiu 1986, Baumann et al. 2000, Oda et al. 2000, Sparg et al.

2004), and lower the surface tension between water and the gills of fish—preventing oxygen uptake and leading to a slow death by oxygen deprivation (Lamba 1970). Fishermen from many cultures have harnessed these effects, using saponin-containing plants as piscicides (Applebaum and Birk 1979, Herlt et al. 2002). The known effects of tannins and saponins on the digestion, respiration, and overall physiology of multiple aquatic species suggest that larval amphibian performance may also be impacted by plant-derived compounds. Similar to fish, many larval amphibians are obligate gill breathers (Burggren and Infantino 1999) or possess a limited ability to compensate for gill damage (Ultsch et al. 1999). To our knowledge, only one previous study has directly tested the effect of plant-derived secondary compounds on amphibian performance, demonstrating that high levels of soybean-derived saponins reduce the survival of *Pseudaepidalea viridis* (syn: *Bufo viridis*, European green toad) under laboratory conditions (Ishaaya et al. 1969).

If the chemical profile of a plant species affects the fitness of aquatic organisms, it follows that changes to the plant community may have ecological impacts. Invasion of non-native plant species is considered a major driver of current habitat change and deterioration (Vitousek et al. 1996); consequently, an increasing amount of resources are dedicated to invasive plant control (D'Antonio et al. 2004, Pullin and Knight 2005). However, it remains unclear whether non-native species are always functionally distinct from native species in their impacts on ecosystem processes (Thompson et al. 1995, van Kleunen et al. 2010). Prior studies that address the relationship between plant species and larval amphibian performance have not separated plant species identity from the trait of interest, such as phytochemistry or native/non-native origin (e.g. Skelly et al. 2002, Maerz et al. 2005, Brown et al. 2006, Schiesari 2006, Williams et al. 2008)—it is therefore difficult to pinpoint a mechanism that explains the impact of plant identity on larval amphibians. Here we describe two

mesocosm experiments that test (1) whether plant-derived secondary compounds impact larval amphibian performance, and (2) whether native/non-native plant origin explains amphibian performance.

In experiment 1, we reared larval *Ambystoma maculatum* (yellow-spotted salamander) and *Lithobates palustris* (pickerel frog) in an aqueous gradient of purified tannin or saponin. We chose tannins and saponins because they are well-characterized, commercially available classes of compounds that are produced by many plant species that co-occur with *A. maculatum* and *L. palustris*. In experiment 2, we reared larval *A. maculatum* in leachate of senescent *Phragmites australis* (common reed) leaves. *Phragmites australis* exhibits high levels of intraspecific variation for a number of plant traits (Hansen 2007)—here we harness this intraspecific variation, as well as the co-occurrence of both native and non-native *P. australis* populations in North America (Saltonstall 2002), as tools to explore the impact of phytochemistry on amphibian larvae. This experimental set-up allows us to separate the effect of plant origin (native/non-native) from plant trait (secondary chemistry). It also allows us to assess whether specific compounds are correlated with amphibian performance using liquid chromatography-mass spectrometry (LC-MS) analysis. We were guided in our work by the following null hypotheses:

H1: Amphibian performance will be independent of tannin or saponin concentrations

H2: Amphibian performance will not be affected by *P. australis* leachates derived from various populations

H3: There will be no difference in mean amphibian performance between leachate derived from native and non-native *P. australis*

Methods

We conducted two outdoor mesocosm experiments from May-August 2009. Although mesocosm set-ups do not capture the complexity of natural systems (Carpenter 1996, Skelly and Kiesecker 2001), results often hold true under field conditions (Resetarits and Fauth 1998, Boone et al. 2004), and unlike field settings, the design allows for a manipulation of single variables (Rowe and Dunson 1994, Boone and James 2005, Chalcraft et al. 2005).

Phragmites australis is the most widespread angiosperm in the world, and expresses intraspecific variation in traits such as photosynthetic potential, salinity tolerance, morphology, and growth strategy (Hansen et al. 2007, Park and Blossey 2008)—we therefore predicted that populations would also vary in phytochemistry. In North America, two “types” of *P. australis* co-occur—a native subspecies *P. australis americanus* and a non-native invasive type that was introduced in the late 1800s and has since spread dramatically (Saltonstall 2002). Non-native *P. australis* is now considered a high-priority invasive species in many states, and is assumed to provide poor quality habitat (Meyerson et al. 2000). *Ambystoma maculatum* and *L. palustris* are found in high abundance in the Eastern United States (Hulse et al. 2001), and *P. australis* can be common at their breeding sites.

We collected *A. maculatum* and *L. palustris* egg clutches on 21 April and 6 May respectively from the Cornell University Arnot Forest in Van Etten, NY (42.291977 N, 76.651890 W). We immediately transported egg clutches to the Cornell University Resource Ecology and Management Laboratory, where we held clutches individually in 6 L plastic containers that floated in a large outdoor pond. We changed water every 2-4 days and fed hatching larvae with fish flakes *ad libitum*. We placed individuals into treatments one week after hatching. In both experiments (saponin/tannin experiment and *P. australis* leachate), we reared individual larvae of

either *A. maculatum* or *L. palustris* in 1 L plastic containers that were floated in outdoor ponds to buffer against temperature fluctuation. We arranged containers in a block design, randomized by clutch and treatment, across 5-10 ponds per experiment. To protect the experiments from rainfall and predation, we covered containers with a fine mesh and covered ponds with a clear plastic roof. Outdoor rearing allows for natural photoperiod and temperature fluctuation, important cues of amphibian metamorphosis. We added large pebbles to the 1 L containers on 10 June in order to add structural complexity. Every two weeks we recorded the water temperature, dissolved oxygen, conductivity, and pH of a subset of containers (5 reps/treatment) with a YSI 556 MPS (YSI Environmental, Yellow Springs, OH).

We fed individuals *ad libitum* (*A. maculatum*: *Daphnia pulex*, amphipod spp. and chironomid spp.; *L. palustris*: TopFin tropical flakes (Franklin WI) and Mazuri Rabbit Diet (Brentwood MO), and colonizing algal spp.). In both experiments, we scored survival every 2-3 days. We staged *A. maculatum* during weeks 2, 5, and 10. Stage series allow for the description of development in discrete steps. The literature on developmental stages of salamanders is far less extensive than for frog development (Donavan 1980); here we use an expanded version of the Harrison series, the Donovan series, which describes developmental stages from the uncleaved egg through metamorphosis (Donavan 1980). We used the Gosner series (Gosner 1960) to stage *L. palustris* larvae at week 10. We recorded snout-vent length (SVL) of both species at week 10. Final data were taken on 20 July for *A. maculatum* (week 10) and 13 August for *L. palustris* (week 10).

Experiment 1

In order to observe the effect of tannin and saponin on larval performance, we reared *A. maculatum* and *L. palustris* larvae (N=20/treatment) in concentrations of 1,

5, 10, 15, 20, or 25 mg/L water of commercially purified saponin (Sigma 84510, 8-25% sapogenin) or tannic acid (Sigma 16201). Approximately one week after hatching, we randomly selected 20 individuals from 5 clutches (4 reps/clutch) for each treatment and placed them into the 1 L containers (*A. maculatum*: 15 May, Harrison stage 40, N=260; *L. palustris*: 8 June, Gosner stage 26, N=260). We compared these treatments to a control group of larvae raised in aged and filtered tap water that was otherwise handled in an identical manner. We based concentrations of tannic acid and saponin on field observations of Maerz et al. (2005), who sampled 13 northeastern wetlands during the *L. palustris* larval development season, finding concentrations of reactive phenolic compounds to range from 1-11 mg/L.

Experiment 2

In order to observe the effect of plant-litter leachate on larval amphibian performance, we reared *A. maculatum* in leachate of *P. australis* leaves collected from multiple populations. Senescent native and non-native *P. australis* leaves were harvested between 25 November and 30 December 2008 from 14 *P. australis* populations across the United States (Table 1.1). The set includes 5 native/non-native pairs that were collected within close proximity (1 km) of one another. We immediately dried and stored leaves in dry opaque paper bags until use. We prepared leachate by gently rinsing off the litter material with water (to dislodge any sediment) and then leaching randomly selected leaves from a *P. australis* population for 48 hours in aged and filtered water. We used a litter-to-water ratio of 1 g/L, which approximates natural litter inputs in New York state (J. Dietrich, unpublished data) and is similar to concentrations used in previous experiments (Maerz et al. 2005, Brown et al. 2006). We then filtered out all plant litter and transferred leachate to the 1 L rearing cups. As a control, we aged and filtered water in a manner identical to plant

leachate. Water for all treatments was filtered with the same filter and stocked randomly in an effort to homogenize potential introduction of any fungal or bacterial pathogens. Approximately one week after hatching, we moved 30 individuals randomly selected from 10 clutches to each treatment (3 reps/clutch, N=450). During the course of the experiment the leachate in each 1 L container was replaced every 20 days. Final data were taken on 20 July (week 10).

Table 1.1: Description of *Phragmites* populations used in Experiment 2

Population	Abbrev	Type	Lat	Long
Agawam Lake, MA	MA N	Native	42.2664	73.3266
Agawam Lake, MA	MA M	Introduced	41.5857	70.6371
Blackstone River, RI	RI M	Introduced	41.9763	71.4838
Syracuse, NY	NY S	Introduced	43.0777	76.0493
Waubay NWR, SD	SD N	Native	45.4114	97.3614
Nonesuch River, ME	ME M	Introduced	43.5561	70.3320
Nonesuch River, ME	ME N	Native	43.5610	70.3297
Aransas NWR, TX	TX I	Native	28.3024	96.8061
Eastern VA Rivers NWR	VA M	Introduced	37.9173	76.8591
Eastern VA Rivers NWR	VA N	Native	38.0710	76.9401
Douglas County, WI	WI N	Native	46.4180	92.0847
Douglas County, WI	WI M	Introduced	46.4899	92.1833
Caldwell Pond, NY	NY N	Native	43.6997	76.1893
Caldwell Pond, NY	NY M	Introduced	43.6988	76.1906

LC-MS analysis

We analyzed *P. australis* leachate using LC-MS technology in order to determine whether the concentration of any plant-derived compound is correlated with *A. maculatum* survival. We created a concentrated leachate by leaching 5g of *P.*

australis leaves in 1 L aged tap water for 72 hours (3 replicates/treatment) at ambient temperature. We then took a 1 mL sample from each treatment, adding 1 mL methanol and vortexing to separate out proteins and freezing at -20°C until analysis. We analyzed samples with HPLC-MS on a Quantum Access triple quadrupole system (Thermo Finnigan LLC, San Jose, CA). Compounds were separated on a ThermoFisher Accela HPLC equipped with a Gemini C18 reversed phase column (3µm, 150 x 4.6 mm, Phenomenex, Torrance, CA) using a solvent gradient (solvent A: 0.1% formic acid in water; solvent B: 0.1% formic acid in acetonitrile): 0-4 min 5% B, 24 min 60% B; 34 min 95% B, 40 min 95% B at a flow rate of 0.7 mL min⁻¹. The MS detector was equipped with an electrospray ionization (ESI) probe operated under the following conditions: spray voltage 5 kV, capillary temperature 390°C, sheath gas (N₂) pressure 40 arbitrary units, auxiliary gas (N₂) pressure 5 arbitrary units. Mass spectra were recorded in positive mode between m/z 100 and m/z 1200 to determine molecular ions [M+H]⁺.

For automated baseline correction, mass spectra extraction, and subsequent spectral data alignment, we split the samples into two groups, high survival (30-50% survival) and low survival (10-30% survival). LC-MS datasets were processed simultaneously using the MetAlign software package (<http://www.metalign.wur.nl/>, Vorst et al. 2005, de Vos et al. 2007), which we programmed to report differences in concentration between the two groups that are ≥ 2 ($P \leq 0.05$). We calculated the peak areas of the resulting dataset with the ThermoFinnigan Xcalibur data system.

Statistical analysis

In order to determine whether abiotic conditions were significantly different among any treatments within an experiment, we compared mean temperature (°C), pH, conductance (µS) and dissolved oxygen (mg/L) on all sample dates using one-way

ANOVA. We fit a nominal logistic regression with pond, clutch, and treatment as fixed effects in order to determine how well these variables predicted probability of survival in experiments 1 and 2 (SAS 9.2, SAS Institute Inc., Cary, NC, USA). We fit a linear regression by least squares with pond, clutch and treatment as fixed effects in order to determine how well these variables predicted measures of performance other than survival in both experiments (measures for *A. maculatum*: Donavan stage at weeks 2, 5, 10, final SVL; for *L. palustris*: final Gosner stage, SVL) (JMP 8.0, SAS Institute Inc., Cary, NC, USA). We compared treatment least square means for significant variables using the Tukey-Kramer HSD test ($\alpha = 0.05$).

To test for differences between native and non-native *P. australis* treatments, we conducted ANOVA of Donavan stage at weeks 2, 5, 10, and final SVL, testing for differences between groups with a Student's t-test. To compare the probability of survival between native and non-native *P. australis*, we conducted a nominal logistic regression with pond, clutch, and native/non-native origin as fixed effects. To compare the peak areas of compounds identified by LC-MS analysis, we compared two survival groups (high survival, low survival) using ANOVA followed by a t-test (3 samples/treatment).

Results

Mean temperature, pH, conductance, and dissolved oxygen were not significantly different among treatments in either experiment, except for experiment 1 on 18 May, at which point mean pH was higher than the control in the 10,15,20,and 25 mg/L saponin treatments and lower than the control in all tannin treatments ($F_{6,34}=39.10$, $P=<0.0001$). Mean pH did not significantly differ among treatments on any subsequent measurement days—we therefore discount temperature, pH, conductance, and dissolved oxygen as explanatory variables.

Experiment 1: Effect of saponin on larval performance

Parameters of each model derived from Experiment 1 are presented in Table 1.2, and measures of larval performance that are significantly different than the control are presented in Table 1.3.

Both *A. maculatum* and *L. palustris* survival were decreased in the highest saponin treatments. Probability of *L. palustris* survival is significantly predicted by saponin treatment, but not clutch or pond, and is significantly lower in the 25 mg/L saponin treatment than the control. Probability of *A. maculatum* survival is predicted by pond, but not saponin treatment or clutch, and is significantly lower in the 20 mg/L and 25 mg/L treatments than the control (Figure 1.1).



Saponin treatment predicts *A. maculatum* developmental stage at weeks 5 and 10, but not the first measurement at week 2. At week 5, mean Donovan stage is slightly but significantly lower in the 10, 15, 20 and 25 mg/L treatments than in the control. At week 10, mean Donovan stage is significantly lower in the 25 mg/L treatment than the control. Pond significantly predicts to Donovan stage at week 10, but not weeks 2 or 5. Clutch does not predict Donovan stage on any measurement day. Neither saponin treatment, pond, nor clutch predict final *A. maculatum* SVL.

Saponin treatment predicts final *L. palustris* Gosner stage as well as final SVL. Neither clutch nor pond explains a significant proportion of these two measures. Mean Gosner stage is significantly lower in the 20 and 25 mg/L saponin treatments than in the control. Mean SVL is significantly lower in the 5, 10, 15, 20 and 25 mg/L treatments than in the control (Figure 1.2).

Table 1.2: Parameters of models for logistic and linear regressions of *A. maculatum* and *L. palustris* performance in Experiment 1 with treatment, clutch, and pond as fixed effects. Significant explanatory variables are shown in bold.

Measure	Model Type	Full model			Treatment		Clutch		Pond	
		R ² _{adj}	Distribution	P	Distribution	P	Distribution	P	Distribution	P
Saponin <i>L. palustris</i> survival <i>A. maculatum</i> survival <i>A. maculatum</i> stage wk 2 <i>A. maculatum</i> stage wk 5 <i>A. maculatum</i> final stage <i>A. maculatum</i> final SVL <i>L. palustris</i> final stage <i>L. palustris</i> final SVL	Logistic	0.18	$\chi^2=34.32$, df=13	0.0011	$\chi^2=28.52$, df=6	<0.0001	$\chi^2=4.84$, df=3	0.1840	$\chi^2=2.34$, df=4	0.6720
	Logistic	0.14	$\chi^2=25.49$, df=13	0.0199	$\chi^2=8.78$, df=6	0.1900	$\chi^2=0.44$, df=3	0.9320	$\chi^2=17.78$, df=4	0.0014
	Linear	0.16	F _{13,135} =1.78	0.0490	F _{6,135} =1.97	0.0700	F _{3,135} =0.44	0.7200	F _{4,135} =2.18	0.0800
	Linear	0.35	F _{13,90} =4.88	0.0010	F _{6,90} =9.56	<0.0001	F _{3,90} =0.87	0.4560	F _{4,90} =0.94	0.4450
	Linear	0.33	F _{13,83} =4.12	<0.001	F _{6,83} =6.55	<0.0001	F _{3,83} =0.37	0.7770	F _{4,83} =5.11	0.0011
	Linear	0.09	F _{13,83} =0.53	0.9010	F _{6,83} =0.70	0.6480	F _{3,83} =0.37	0.7730	F _{4,83} =0.39	0.8170
	Linear	0.23	F _{13,81} =2.87	0.0024	F _{6,81} =4.20	0.0012	F _{3,81} =1.84	0.1480	F _{4,81} =3.04	0.2020
	Linear	0.43	F _{13,83} =5.62	<0.0001	F _{6,81} =10.63	<0.0001	F _{3,81} =1.46	0.2310	F _{4,81} =0.39	0.8180
	Tannin <i>L. palustris</i> survival <i>A. maculatum</i> survival <i>A. maculatum</i> stage wk 2 <i>A. maculatum</i> stage wk 5 <i>A. maculatum</i> final stage <i>A. maculatum</i> final SVL <i>L. palustris</i> final stage <i>L. palustris</i> final SVL	Logistic	0.18	$\chi^2=27.87$, df=13	0.0094	$\chi^2=20.89$, df=6	0.0019	$\chi^2=1.38$, df=3	0.7110	$\chi^2=6.51$, df=4
Logistic		0.1	$\chi^2=17.37$, df=13	0.1830	$\chi^2=10.11$, df=6	0.1200	$\chi^2=2.24$, df=3	0.5240	$\chi^2=6.72$, df=4	0.1520
Linear		0.11	F _{13,133} =2.28	0.0100	F _{6,133} =2.71	0.1030	F _{3,133} =1.17	0.3250	F _{4,133} =0.40	0.3980
Linear		0.28	F _{13,97} =3.89	<0.0001	F _{6,97} =7.87	<0.0001	F _{3,97} =0.13	0.9440	F _{4,97} =0.30	0.8780
Linear		0.28	F _{13,75} =3.29	0.0008	F _{6,75} =4.12	0.0003	F _{3,75} =2.31	0.0847	F _{4,75} =0.66	0.6240
Linear		0.15	F _{13,75} =0.81	0.6470	F _{6,75} =1.36	0.2470	F _{3,75} =1.49	0.8960	F _{4,75} =0.53	0.7130
Linear		0.17	F _{13,105} =2.61	0.0039	F _{6,105} =3.75	0.0022	F _{3,105} =2.69	0.0506	F _{4,105} =0.93	0.4510
Linear		0.12	F _{13,105} =2.19	0.0157	F _{6,105} =2.27	0.0535	F _{3,105} =3.55	0.0175	F _{4,105} =0.251	0.2510

Table 1.3: Measures of amphibian fitness by saponin and tannin concentration. “S” indicates that the saponin treatment was significantly lower than the control ($P < 0.05$). “T” indicates that the tannin treatment was significantly lower than the control. Means \pm standard error shown in parentheses.

(mg/L)	<i>L. palustris</i> 			<i>A. maculatum</i> 			
	Survival	Final Gosner stage	Final SVL (mm)	Survival	Donavan Stage wk 2	Donavan Stage wk 5	Final Donavan Stage
0	(75%)	(26.09 \pm 0.18)	(1.22 \pm 0.036)	(75%)		(48.77 \pm 0.24)	T (49.34 \pm 0.14)
1							
5			S (1.01 \pm 0.036)				T (48.33 \pm 0.21)
10		T (25.35 \pm 0.18)	S (1.00 \pm 0.034)			S (47.94 \pm 0.27) T (47.00 \pm 0.27)	T (48.40 \pm 0.18)
15		T (25.68 \pm 0.21)	S (0.90 \pm 0.064)			S (47.37 \pm 0.27) T (47.34 \pm 0.27)	T (48.43 \pm 0.19)
20		S (25.09 \pm 0.22) T (25.37 \pm 0.17)	S (0.87 \pm 0.043)	S (35%)		S (46.93 \pm 0.35) T (46.72 \pm 0.33)	T (48.20 \pm 0.22)
25	S (35%) T (50%)	S (24.92 \pm 0.27) T (24.46 \pm 0.22)	S (0.80 \pm 0.054)	S (40%) T (30%)		S (46.62 \pm 0.31) T (46.24 \pm 0.34)	S (48.04 \pm 0.18) T (48.16 \pm 0.26)

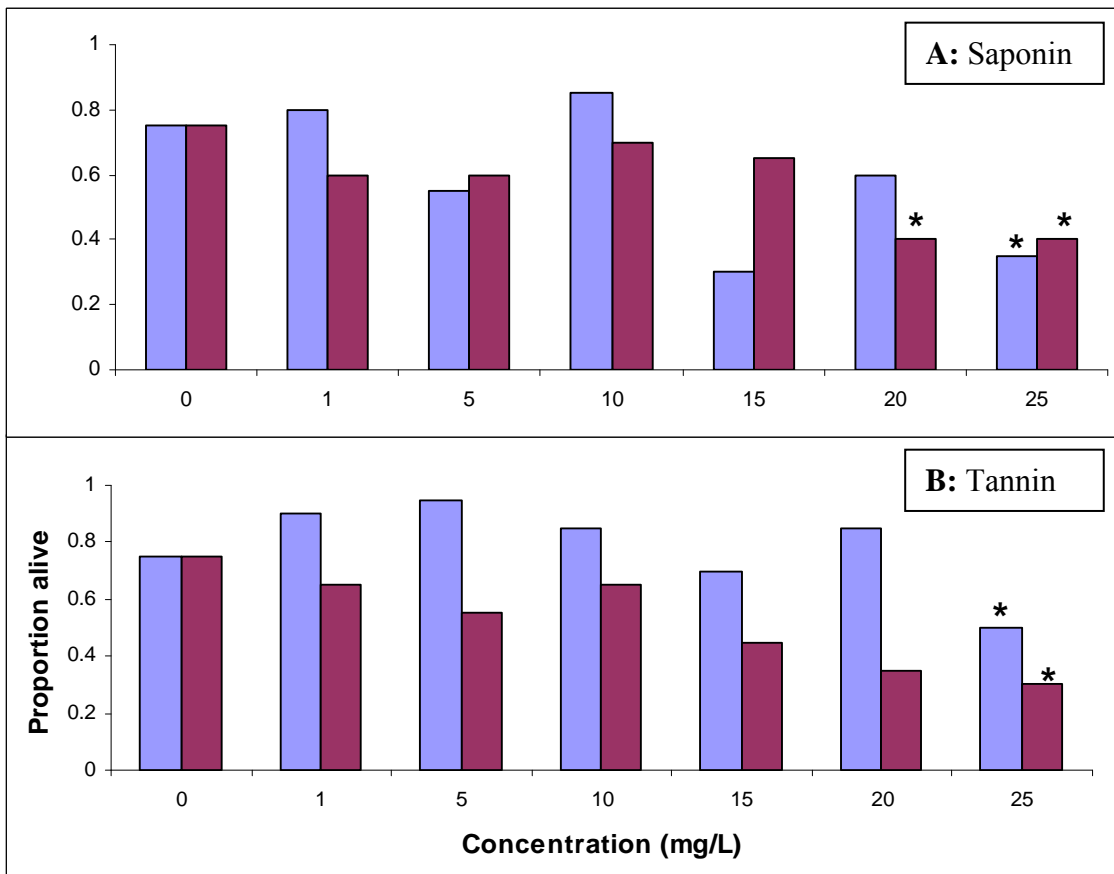


Figure 1.1: Final survival (proportion alive) of *L. palustris* (blue) and *A. maculatum* (purple) by concentration (mg/L) of saponin (A) or tannin (B). N=30 individually reared larvae/treatment/species. * indicates significant difference from the control.

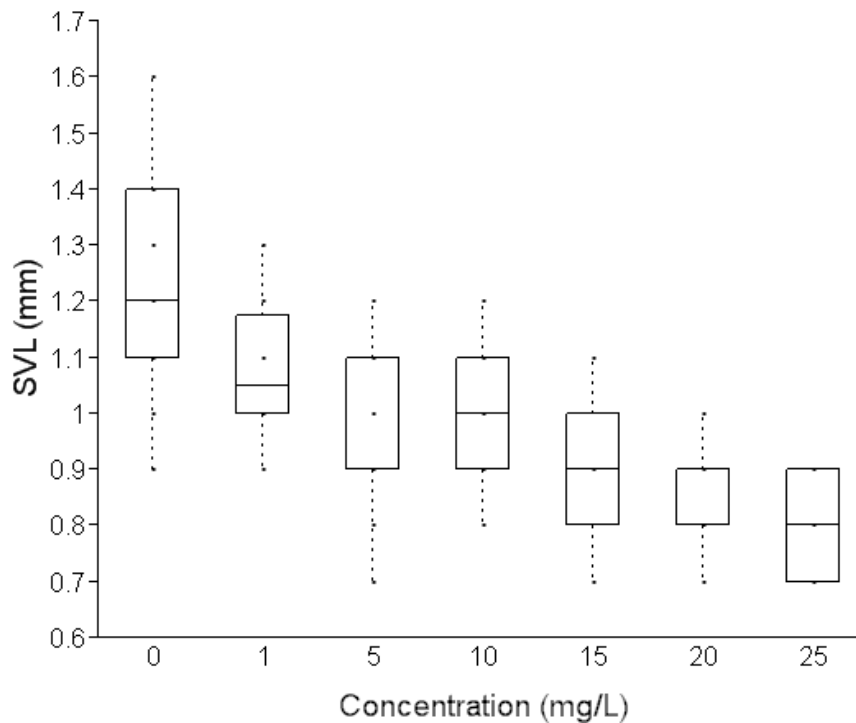


Figure 1.2: Box plots (displaying median, 25-75 percentile, and range) of *Lithobates palustris* final SVL (mm) as a function of saponin concentration (mg/L). N=5-17 individually reared larvae/treatment.

Experiment 1: Effect of tannin on larval performance

Both *A. maculatum* and *L. palustris* survival were decreased in the highest tannin treatments. Probability of *L. palustris* survival is predicted by tannin treatment, but not clutch or pond, and is significantly lower in the 25 mg/L treatment than the control. Probability of *A. maculatum* survival is not significantly predicted by tannin treatment, clutch, or pond—probability of survival is lower in the 25 mg/L treatment than the control (Figure 1.1).

Tannin treatment, but not clutch or pond, predicts *A. maculatum* development stage at weeks 5 and 10, but not week 2. At week 5, mean Donavan stage is significantly lower in the 10, 15, 20 and 25 mg/L treatments than in the control. At week 10, mean Donavan stage is significantly lower in the 5, 10, 15, 20 and 25 mg/L treatments than in the control. Neither tannin treatment, pond, nor clutch predict final *A. maculatum* SVL.

Tannin treatment but not pond or clutch predicts final *L. palustris* Gosner stage. Mean final Gosner stage is significantly lower in the 10, 15, 20 and 25 mg/L treatments than the control. Mean *L. palustris* final SVL is significantly predicted by clutch but not tannin treatment or pond.

Experiment 2: Effect of *P. australis* leachate on *A. maculatum* performance

Parameters of each model derived from Experiment 2 are presented in Table 1.4, and measures of larval performance that are significantly different than the control are presented in Tables 1.5 and 1.6.

Probability of *A. maculatum* survival was significantly lower than the control in 9 of the 14 *P. australis* populations. Probability of survival is predicted by *P. australis* population and clutch, but not pond. Metamorphic stage at weeks 2 and 5 is predicted by *P. australis* population and clutch, but not pond. At week 10, *P. australis* population but not clutch or pond predicts metamorphic stage. Developmental stage is significantly lower than the control in 4 *P. australis* populations at week 2, 8 populations at week 5, and 4 populations at week 10. Neither *P. australis* population, clutch, or pond predict final SVL. Mean SVL is significantly lower than the control in 6 of 14 *P. australis* populations.

There is no significant difference between native and non-native treatments in mean *A. maculatum* developmental stage at week 2 ($F_{1,408}=0.0154$, $P=0.901$), week 5

Table 1.4: Parameters of models for logistic and linear regressions of *A. maculatum* performance in Experiment 2 with treatment, clutch, and pond as fixed effects. Significant explanatory variables are shown in bold.

Measure	Model Type	Full model			Treatment		Clutch		Pond	
		R^2_{adj}	Distribution	<i>P</i>	Distribution	<i>P</i>	Distribution	<i>P</i>	Distribution	<i>P</i>
<i>A. maculatum</i> survival	Logistic	0.16	$\chi^2=98.87$, df=32	<0.0001	$\chi^2=23.49$, df=14	0.0528	$\chi^2=70.01$, df=9	<0.0001	$\chi^2=10.96$, df=9	0.3600
<i>A. maculatum</i> stage wk 2	Linear	0.13	$F_{32,438}=2.92$	<0.0001	$F_{14,438}=2.41$	0.0030	$F_{9,438}=2.41$	<0.0001	$F_{9,438}=2.41$	0.1586
<i>A. maculatum</i> stage wk 5	Linear	0.22	$F_{32,193}=2.65$	<0.0001	$F_{14,193}=3.56$	<0.0001	$F_{9,193}=2.84$	0.0039	$F_{9,193}=0.96$	0.4760
<i>A. maculatum</i> final stage	Linear	0.13	$F_{32,179}=1.81$	0.0099	$F_{14,179}=2.31$	0.0066	$F_{9,179}=0.78$	0.6320	$F_{9,179}=2.31$	0.2090
<i>A. maculatum</i> final SVL	Linear	0.22	$F_{32,179}=1.37$	0.1060	$F_{14,179}=1.57$	0.0940	$F_{9,179}=1.47$	0.1650	$F_{9,179}=0.95$	0.4810

Table 1.5: Differences of least square means for probability of *A. maculatum* survival between control and all other treatments.

Phragmites australis treatments that are significantly different from the control are bolded.

Treatment 1	Treatment 2	Diff	St Error	χ^2	Pr> χ^2
Control	MA M	1.4900	0.5925	6.32	0.0119
Control	MA N	0.9451	0.5856	2.60	0.1066
Control	ME M	1.1514	0.5909	3.80	0.0514
Control	ME N	1.6566	0.5947	7.76	0.0053
Control	NY M	1.4552	0.5991	5.90	0.0151
Control	NY N	1.6811	0.6065	7.68	0.0056
Control	NY S	2.4227	0.6448	14.12	0.0002
Control	RI M	1.8281	0.6155	8.82	0.0030
Control	SD N	1.6811	0.6065	7.68	0.0056
Control	TX I	0.9930	0.5804	2.93	0.0871
Control	VA M	1.1385	0.5861	3.77	0.0521
Control	VA N	1.3058	0.5979	4.77	0.0290
Control	WI M	1.3119	0.5881	4.98	0.0257
Control	WI N	0.8529	0.5808	2.16	0.1419

Table 1.6: Mean measures of *A. maculatum* performance by *Phragmites* population. Levels not connected by same letter are significantly different (Tukey-Kramer HSD, $P < 0.05$). N=5-22 individually-reared larvae/treatment.

Treatment	Total survival		Donavan Stage Wk 2		Donavan Stage Wk 5		Final Donovan Stage		Final length (mm)	
	Survival	Mean	Letter	Mean	Letter	Mean	Letter	Mean	Letter	Mean
Control	A	0.73	A	46.2	A	48.4	A	49.5	A	13.1
VA M	A	0.47	CD	45.6	BC	47.4	AB	49.0	ABC	13.8
WI N	A	0.50	BC	45.7	BCDE	47.3	B	48.6	A	13.1
ME M	A	0.43	CD	45.6	BC	47.6	B	48.9	AB	13.2
MA N	A	0.50	BCD	45.6	BCDE	47.0	B	48.7	ABC	13.9
TX I	A	0.50	CD	45.6	BC	47.4	B	48.5	ABC	13.4
SD N	B	0.33	BC	45.8	DE	46.6	B	48.6	ABC	13.4
RI M	B	0.30	CD	45.6	E	46.5	B	48.6	BC	14.8
MA M	BC	0.37	AB	46.0	BCDE	47.1	AB	49.0	BC	14.7
VA N	BC	0.43	CD	45.6	CDE	46.8	B	48.7	ABC	13.9
ME N	BC	0.33	CD	45.6	BCDE	46.8	B	48.5	ABC	14.5
WI M	BC	0.40	D	45.3	B	47.6	B	48.7	BC	14.7
NY M	BC	0.37	CD	45.6	BCD	46.8	B	48.6	BC	14.8
NY N	BC	0.37	CD	45.6	BCD	47.4	B	48.5	BC	14.8
NY S	C	0.17	CD	45.5	BCDE	46.8	B	48.6	C	15.2

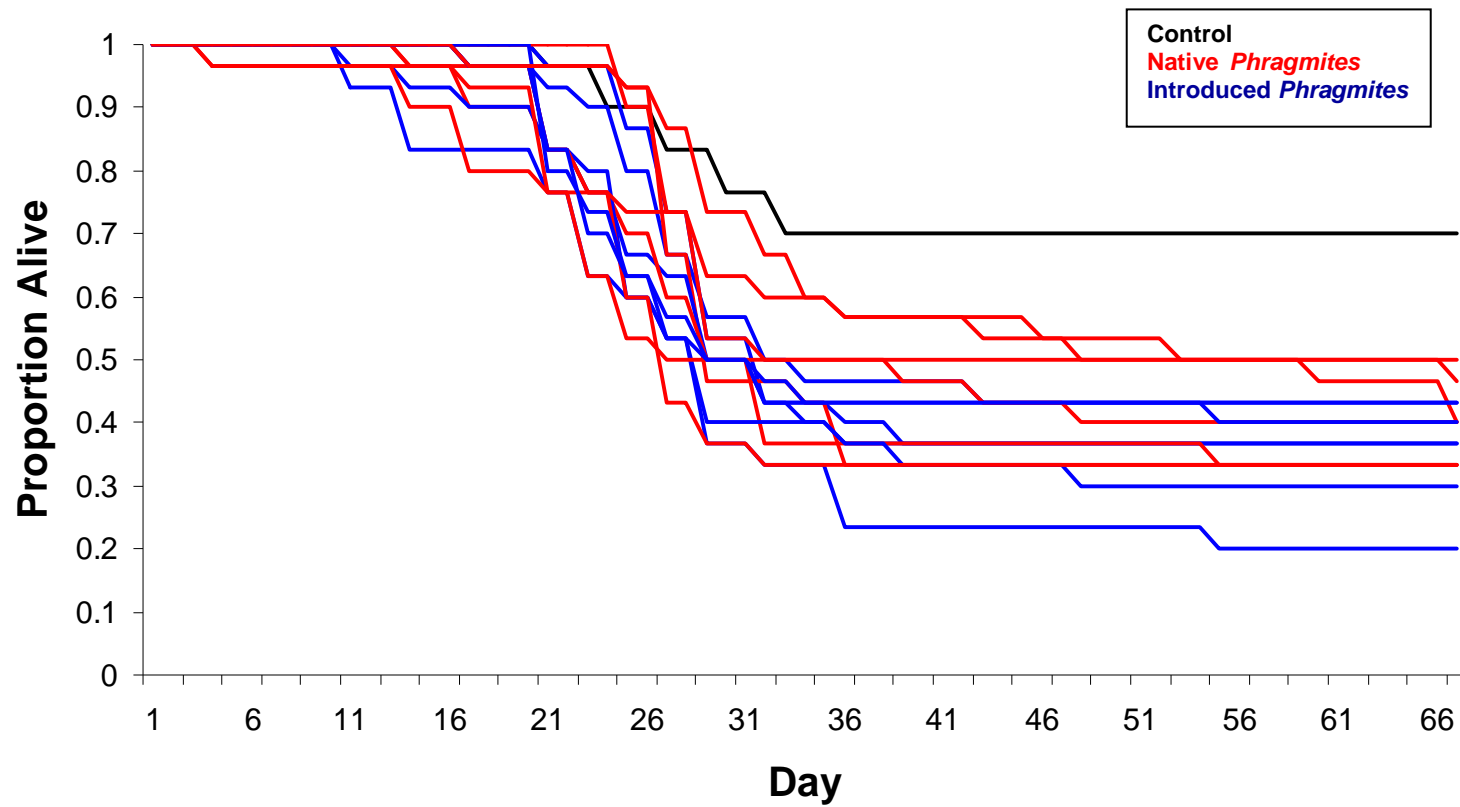


Figure 1.3: *Ambystoma maculatum* survival (proportion alive) by treatment (native or introduced *Phragmites* leachate) and day. N=30 individually reared larvae/treatment/species.

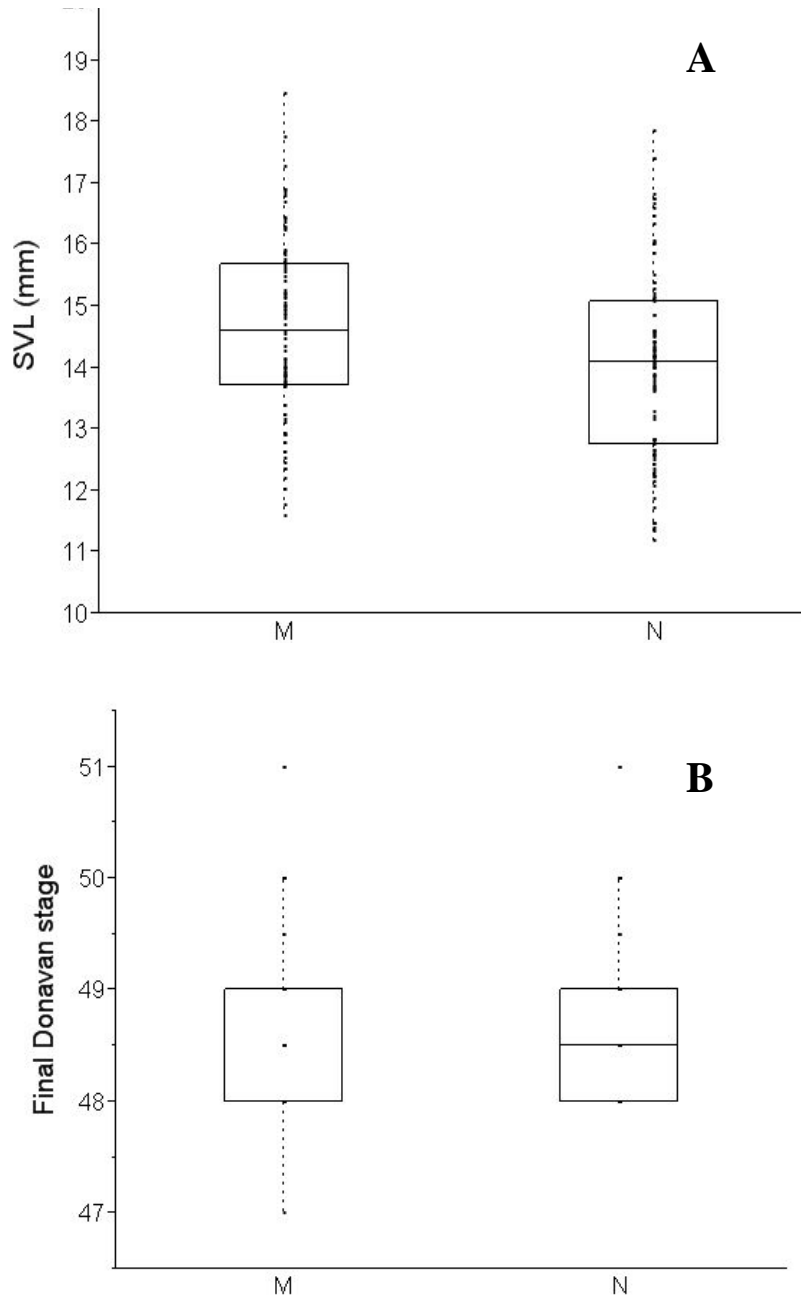


Figure 1.4: Final *A. maculatum* SVL (A) and stage (B) by non-native (M) or native (N) origin of the *Phragmites* litter. N=5-22 individually reared larvae/treatment (7 native treatments, 7 non-native treatments).

($F_{1,173}=0.694$, $P=0.406$), or week 10 ($F_{1,159}=3.14$, $P=0.080$), nor is there a difference in final SVL ($F_{1,169}=2.79$, $P=0.097$) (Figure 1.4). Probability of *A. maculatum* survival is predicted by clutch ($\chi^2=68.42$, $df=9$, $P<0.0001$) but not native/non-native status ($\chi^2=1.40$, $df=1$, $P=0.236$) or pond ($\chi^2=9.48$, $df=9$, $P=0.487$) (model: $R^2_{adj}=0.14$, $\chi^2=77.51$, $df=19$, $P<0.0001$) (Figure 1.3).

Experiment 2: Correlation of LC-MS output with *A. maculatum* performance

The MetAlign program generated a dataset of 353 candidate compounds that have significantly different mean peak areas between the low survival and high survival groups. In further manual calculations, we found that peak area is significantly different between groups for only one compound—mass 565, retention time 13.35 minutes ($F_{1,42}=8.82$, $p=0.014$). Peak areas for this compound are approximately 8 times larger in the low survival group than the high survival group (Figures 1.5,1.6).

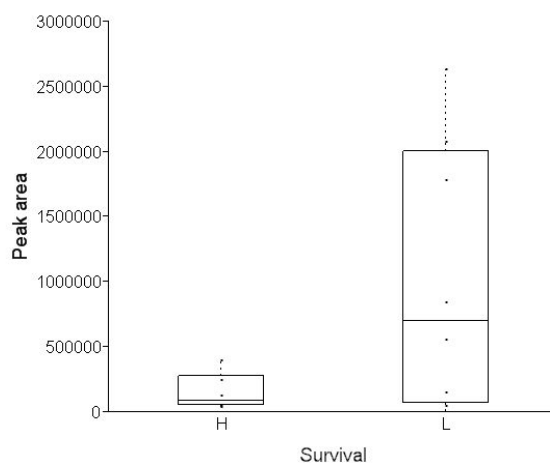


Figure 1.5: Box plots (median, 25-75 percentile, range) of peak areas between the high (H: 30-50% total survival) and low (L: 10-30%) survival groups (3 reps/treatment, N=42) for the unidentified compound at mass=565, retention time=13.35 min.

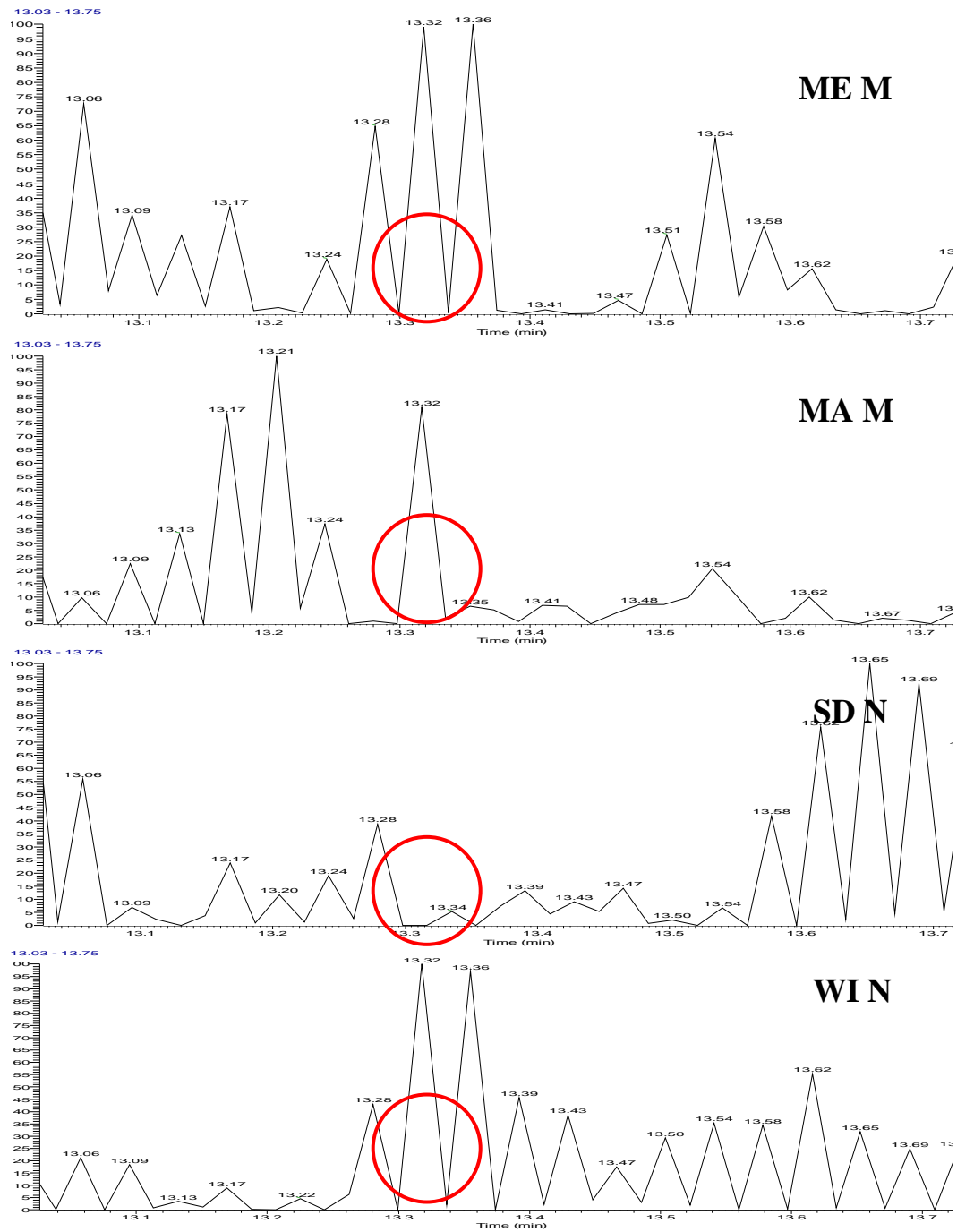


Figure 1.6: Example HP-LC chromatographs showing peak area (y axis) at mass=565 at a retention time 12-14 minutes (x-axis) by *P. australis* population. Circles indicate the compound that is significantly correlated with high or low survival.

Discussion

Taken together, the results of experiment 1 and 2 demonstrate that plant-derived compounds affect the survival and development of larval amphibians. Experiment 2 demonstrates that a plant trait (phytochemistry) better explains *A. maculatum* performance than plant origin (native or non-native). In prior experiments, plant species identity has not been separated from the effect of specific traits (e.g. Skelly et al. 2002, Williams et al. 2008). For example, Williams et al. (2008) reared three species of amphibian larvae in treatments of “grass” (Poaceae and Cyperaceae spp.) or “leaves” (*Quercus* and *Carya* spp.), finding all species to have a lower mass at metamorphosis in the leaf treatment than in the grass treatment. Although the authors suggest that these differences were driven by more rapid decomposition of grass leading to higher food quality, our results suggest that there may also be an effect of differing phytochemistry between treatments.

High concentrations of both tannin and saponin significantly decreased larval survival, and ecologically-realistic concentrations of both compounds decreased rate of metamorphosis and *L. palustris* SVL. Such effects have ramifications on adult fitness—a larger size at metamorphosis is frequently correlated with adult reproductive success (e.g. Blakley 1981, Peters 1983, Davidowitz et al. 2004), and early metamorphosis often leads to increased fitness if an individual escapes predation (Wilbur and Collins 1973, Werner 1986, Relyea 2007) or if reproducing earlier increases resources available to offspring (Smith 1987, Semlitsch et al. 1988, Fischer and Fielder 2002). Although our results suggest that larval exposure to tannin, saponin, and *Phragmites* leachate will impact adult fitness, we cannot determine the physiological mechanism behind the impact. The fact that death occurred gradually throughout the experiment suggests the “slow death by oxygen deprivation” that occurs when saponin lowers the surface tension between water and fish gills (Lamba

1970). The experimental treatments likely compounded the effects of an already-stressful mesocosm environment—the results must be considered relative to the water control, in which there was approximately 25% mortality. The additional stress of limited food supply has been shown to exacerbate the negative effect of *Lythrum salicaria* extract on *Bufo americanus* (Maerz et al. 2005). Similarly, our results suggest that the presence of certain plant compounds may be exacerbated by other stressors (in this case the stress of a mesocosm environment).

Despite the stress of a mesocosm environment, we expect that our results are applicable to natural conditions. A study comparing *Bufo americanus* development in *L. salicaria* and *T. latifolia* detritus found consistent results in both mesocosm and field experiments (Brown et al. 2006). In a recent field experiment, Cohen (2009) finds *B. americanus*, *R. sylvatica*, and *R. palustris* performance can be predicted by plant traits, but not the native/non-native origin of the plant species. In our experiment, tannin concentration affected amphibian performance at levels as low as 5 mg/L—a particularly realistic concentration, given that Maerz et al. (2005) recorded reactive phenolic concentrations ranging from 1-11 mg/L in northeastern wetlands. At present no data exist as to saponin concentrations in natural settings.

Early mortality of less-robust individuals may explain why there is no difference in final *A. maculatum* SVL in either saponin or tannin treatments while there is a clear inverse relationship between *L. palustris* SVL and saponin concentration. At the termination of the experiment, *A. maculatum* possessed fully-developed hind limbs (mean Donovan stage = 49), whereas *L. palustris* had developed hind limb buds, but were not near full metamorphosis (mean Gosner stage = 25-26). In a side experiment, we continued to rear 5 *A. maculatum* individuals per treatment in larger (100 L) containers until metamorphosis. There was no further mortality of individuals, suggesting that those individuals remaining in week 10 were those able to

“cope with” their respective treatments. It is possible, however, that we would have continued to observe mortality in *L. palustris*. It is also possible that the saponin treatment impacted *A. maculatum* performance at lower concentrations than *L. palustris* because of the vulnerability of *A. maculatum* external gills. Larval amphibians have been shown to exhibit species-specific responses in other contexts (e.g. Relyea 2003, Skelly et al. 2000)—differences in responses may be explained by differences in respiratory capacity (Ultsch et al. 1999, Brown et al. 2006).

The results of both experiment 1 and 2 highlight the importance of the intraspecific variation exhibited by both plant and amphibian species. Through individual rearing, we were able to separate the effect of clutch from the effect of the treatments. Clutch was a highly significant variable for many of the measurements. If clutch had not been accounted for, it is possible that some of the differences between treatments would have been obscured. Intraspecific variation also accounts for the differential effects of *P. australis* populations on larval amphibian performance “in the afterlife”. This intraspecific variation allowed us to use LC-MS analysis to narrow down the potential phytochemicals that may explain larval survival. Such phytochemicals will inevitably vary between genotypes, and can also vary temporally within a species (e.g. induced defensive compounds, changes in resource allocation).

Today 32% of amphibian species are globally threatened, as compared with 12% of birds and 23% of mammals (Stuart et al. 2004). Research indicates that amphibian decline is explained not just by one factor, but by a combination of stressors (Blaustein and Kiesecker 2002, Kiesecker 2003, Stuart et al. 2004), including invasive species (Beebee and Griffiths 2005). Here we show that certain populations of native *P. australis* can decrease *A. maculatum* larvae survival and metamorphic rate to the same degree as certain non-native *P. australis* populations. Although non-native plant species have been implicated in dramatic habitat change (Mack et al 2000,

Mooney and Hobbs 2000), our phylogenetically-controlled comparison of a native and non-native conspecific suggests that native/non-native origin of a plant species may not be the right unit with which to predict ecological impact to larval amphibians. If a land manager is attempting to manage for a robust amphibian community, it may be better to manage for plant community heterogeneity—a factor that has been shown to be an important predictor of amphibian species richness (Vasconcelos et al. 2009, Parris and McCarthy 1999, Afonso and Eterovick 2007)—than attempting to eradicate a particular non-native species based solely on the assumption that all invasive species have negative ecological impacts. Our results suggest that plant traits, not plant origin, best predict the ecological impact of a novel plant species.

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CHAPTER 2

THE MONETARY AND CHEMICAL COSTS OF INVASIVE PLANT MANAGEMENT

Abstract

Funding for non-native plant species management has increased substantially in recent years; meanwhile, there have been few assessments of management outcomes. Here we present a case study that highlights current obstacles to successful management of non-native plant species and their associated impacts. In a comprehensive survey of 285 land-managers from across the United States, we find that public and private organizations spend at least \$4.6 million per year on *Phragmites australis* (common reed) control. Over 90% of these organizations have applied herbicide in the past five years, treating a total of 80,450 wetland hectares with 940-470,200 L of herbicide. Despite this high expenditure of resources and chemicals, organizations report that they rarely accomplish management objectives. A synthetic understanding of invasive plant management is essential to achieving more economically and ecologically sustainable land stewardship.

Introduction

Over 4,300 non-native species are naturalized in the United States (US OTA 1993); the perceived negative ecosystem impacts of these species (Mack et al 2000, Mooney and Hobbs 2000) have led federal, state, municipal, land trust, and other private organizations to actively manage a subset of “invasive” populations—those defined by the federal government as abundant non-native species that cause economic or environmental harm (US Executive Order 13112). Organizations continue to

increase resources directed towards invasive plant management (D'Antonio et al. 2004, Pullin and Knight 2005)—for example, the U.S. federal budget for invasive species management increased by over \$400 million between 2002 and 2006 (US NISC 2006). Meanwhile, due to a lack of coordination between organizations and infrequent post-control monitoring, we know little about the outcomes of management efforts (US OTA 1993, Blossey 1999, Korfmacher 2000, Panetta and Lawes 2005, Acharya 2009).

Land managers control invasive plants using mechanical (e.g. mowing, cutting), physical (e.g. fire, flooding), chemical (herbicide), or biological methods. Emphasis is often placed on removing the invader rather than managing the invaded ecosystem (Hobbs and Humphries 1995). Implicit to such an approach is the idea that the removal of an invader will result in the restoration of native species and ecosystem processes (Zavaleta et al. 2001). However, invasive species may be systematic of other stressors, rather than the drivers of ecosystem change (MacDougall and Turkington 2005). If the invader has already changed the abiotic or biotic conditions of a site, removal of an invasive species may not be enough to allow ecosystems to recover—in this case control must be followed by site restoration (El-Ghareeb 1999, Zavaleta et al. 2001). It follows that non-native plant control is not necessarily equivalent to native plant protection (Smith et al. 2006).

There have been few synthetic descriptions of the invasive plant management process (US OTA 1993, Reid et al. 2009). Although invasive species are a “public bad,” (Burnett 2006), control is often uncoordinated between organizations and is driven by individual expertise of scientists or managers (US OTA 1993). Funding for invasive plant management is not centralized, and comes from a mixture of small public and private grants that are often dedicated towards a certain species or control method—for example, the BASF Invasive Vegetation Management Matching Grant

Program specifically supports the use of herbicides for invasive plant management (<http://www.basf.com>). Furthermore, without clearly-articulated goals or benchmarks, it is difficult to measure post-management success—most current data on management outcomes are therefore strictly qualitative or anecdotal (Blossey 1999).

Despite the fact that restoration of native species and ecosystem processes are the top goals of invasive plant management, few organizations report success at attaining these goals (Blossey 1999, Denslow and D’Antonio 2005)—for example, Australian land managers report that undesired species invaded recently-managed areas over 50% of the time (Reid et al. 2009), and only 4% of 78 US land managers report success in eliminating invasive plants from their management area (Acharya et al. 2009). Those organizations that rate themselves as more successful in meeting management goals are more likely to continuously monitor invasive and native plants, undergo long-term invasive plant treatments, and actively reseed or replant native plants (Acharya et al. 2009). However, organizations often internally rate success by the number of individual invaders removed rather than the post-control state of the ecosystem (Blossey 1999, Acharya 2009).

In order to obtain an understanding of invasive plant management across organizational types, we conducted a survey of U.S. land managers (federal, state, municipal, land trust, private) on current *Phragmites australis* management methods and outcomes. *Phragmites* is an invasive wetland plant targeted by a number of public and private organizations (see Appendix for description of *Phragmites* and its management). Unlike the majority of economic studies, which focus on agricultural markets (Born et al. 2005, Lovell et. al. 2006, Olson et al. 2006), we report the economic cost of an invasive plant that is managed in natural areas. We then integrate our data on *Phragmites* management into a broader dialogue on invasive plant management.

Methods

We conducted a survey of land managers working for federal (e.g. Fish and Wildlife Service, National Park Service, Army Corps of Engineers), state (e.g. departments of environment, natural resources, agriculture, and transportation), municipal, land-trust (e.g. The Nature Conservancy) and other private organizations (e.g. Ducks Unlimited, consultants). We sent email solicitations to approximately 500 individuals who previously expressed interest in *Phragmites* management, as well as professional list-servs (e.g. Ecological Society of America, invasive plant groups), asking recipients to forward the solicitation email to any appropriate colleagues. We tested a draft survey in a number of pilot interviews with NY state and federal land managers; a modified draft was presented to a focus group of private and public land managers in April 2009. We disseminated the final version online in October 2009. The survey (available from the authors upon request) presented respondents with background material that included a brief overview of *Phragmites* management in the United States, definitions of the terms “biocontrol” and “species abundance,” and an outline of the survey structure.

In the first section, respondents indicated their affiliation (state, federal, municipal, land trust, or other private organization), location, the total area they are involved in managing, their organization’s overall expenditures on *Phragmites* and invasive plant management, and their organization’s *Phragmites* management practices. Estimates of management expenditures included number of hours (inclusive of staff and travel time) spent on *Phragmites* and total invasive plant control in the past five years, as well as cost of *Phragmites* and total invasive plant control in the past five years. We asked for expenditures on a five-year rather than one-year timeframe because many organizations do not have a reliable annual funding

commitment (Acharya 2009). Given the opportunity to provide open-ended feedback at the end of the survey, a number of participants noted that the grants that fund their organization's management efforts are one-time rather than annual grants.

In the second section, we solicited respondents' perceptions of (1) their organization's *Phragmites* management goals, (2) whether *Phragmites* management has been successful regarding a number of metrics, and (3) factors that may constrain *Phragmites* management. These questions were divided into series of sub-questions that respondents rated on a 5-point Likert scale (1=strongly disagree, 5=strongly agree). Goals of *Phragmites* management included ecologically-motivated goals such as restoration of natural hydrology or native plant species, as well as economically-motivated goals such as improvement of tourism. Metrics of success included temporary and long-term control of *Phragmites*, as well as restoration of native species. Factors that may constrain *Phragmites* management included lack of resources, lack of data, and lack of prior success. The options presented in all sub-questions (Tables 1-4) were based on feedback from pretest focus-groups. We also asked respondents whether or not they would accept the use of biocontrol under a number of hypothetical circumstances.

In order to test for differences among respondent affiliations (federal, state, municipal, land trust, private) we conducted a one-way analysis of variance (ANOVA) on the number of hectares of native and non-native *Phragmites* managed by an organization in the past 5 years, *Phragmites* and invasive plant management in hrs/year and hrs/ha/year, *Phragmites* and invasive plant management in dollars/year and dollars/ha/year, and percent of total invasive plant budget and time spent on *Phragmites* management. In order to test whether hours/ha/year or dollars/ha/year spent on *Phragmites* control were significantly correlated with respondent ratings of control success, we performed ordinal logistic regression on each of the ten success

categories (Table 2) with “hours/ha/yr on *Phragmites* control” or “dollars/ha/yr on *Phragmites* control” and “respondent affiliation” as fixed effects. We also compared the distribution of each success rating by whether or not a particular method of control had been employed in the past 5 years. We performed all statistical tests in JMP 8.0 (SAS Institute Inc., Cary, NC).

Results

Participants

We received 285 responses from public and private land-managers involved in invasive plant management across the United States. It is impossible to calculate an exact response rate because we asked recipients of the solicitation email to forward the survey link—however, we can approximate a response rate through descriptive statistics. Native and non-native *Phragmites* is found in 859 counties in 45 states (USDA 2010). Comparatively, surveys were returned from land managers in 40 states, representing 425 counties (Figure 2.1). As it is likely that *Phragmites* is not managed in nearly every county it is found in, we believe that our results represent a large proportion of the organizations that actively manage *Phragmites*. There is better representation of eastern than western states—however, management of *Phragmites* is more common in eastern than western states.

Private organizations provided the greatest number of replies (39%, N=111), followed by federal (24%, N=67), state (23%, N=65), municipal (8%, N=24), and land trust (6%, N=18) organizations. The 285 participants actively manage 0.4 – 22.5 million ha for invasive species (median = 2145 ha); combined, they are responsible for management of ~81 million ha, or 12.3% of the area of the continental United States. This number may seem high, but the federal government alone owns approximately 21.4% of continental U.S. land area. There is no significant difference among

respondent affiliation for any variable—we therefore report results as a single dataset, uncategorized by respondent affiliation.

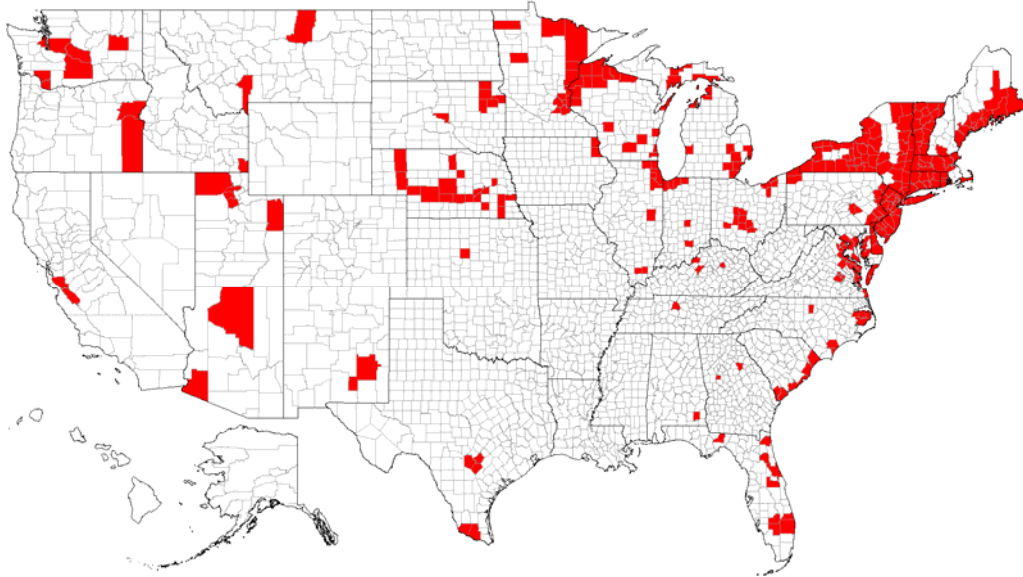


Figure 2.1 Geographical distribution of respondents by county

Invasive plant management

Overall, the organizations captured in this survey spend a combined total of 435,364 hours and \$22,101,000 per year on the management of invasive plant species. Multiplying the median annual wage of a conservation scientist, \$29/hr (US BLS 2010), by the number of hours spent by represented organizations on invasive plant control, we arrive at an aggregate expenditure of approximately \$34,726,000/yr spent on invasive plant control. This result is consistent with other published figures on U.S. expenditures. In 2006, the U.S. federal budget for invasive species control was reported at \$465,906,000 (US NISC 2006).

Invasive plant management budgets reported by participants in our survey ranged from \$0.40-\$5 million/yr (median=\$10,000/yr). Time spent on invasive plant species management ranged from 0.4-156,000 hrs/yr (median=300 hrs/yr). Analyzed by unit area, the represented organizations spend between <0.01-494 hrs/ha/yr on control (median=0.09 hrs/ha/yr) and between \$0.04 - \$19,768/ha/year on control (median=\$2.47/ha/yr).

Phragmites management

Of the 285 respondents, 69% (N=196) report that their organization has actively controlled non-native *Phragmites* in the past five years. Individual respondents are involved in management of between <0.1 - 28,328 ha of non-native *Phragmites* (median=40 ha), for a combined total of 22,566 ha of native *Phragmites* and 89,900 ha of non-native *Phragmites*. The median area suggests that most organizations manage quite extensive areas. The 196 organizations spend a total of 30,553 hrs/yr (total staff hours including travel and planning) and \$3,752,800/yr on non-native *Phragmites* management. Multiplying the median annual wage of a conservation scientist by the number of hours spent on *Phragmites* control, we arrive at an aggregated expenditure of \$4,638,800/yr. Expenditure (<1-800,000/yr; median=\$2000) and time committed to *Phragmites* management (<1-4000 hrs/yr, median=40) vary widely among organizations. Represented as resources per unit area, organizations spend <0.01 - 988 hrs/ha/yr on *Phragmites* control (median=1.65 hrs/ha/yr), and between <1 - \$98,800/ha/yr on *Phragmites* control (median=\$59/ha/yr). *Phragmites* control accounts for 0-100% of reported invasive plant management budgets (median=20%) and 0-100% of hours spent on invasive plant management (median=10%).

The majority (94%, N=185) of organizations that manage *Phragmites* use herbicide as a primary control method. Mowing is the second most common method of control (56%, N=109), followed by herbicide in combination with mowing (52%, N=102), digging by hand (24%, N=48), burning (23%, N=46), herbicide in combination with burning (15%, N=30), flooding (11%, N=23), herbicide in combination with flooding (11%, N=22), and disking (5%, N=10). Both glyphosate (Rodeo, Dow AgroSciences, IN, USA) and imazapyr (Habitat, BASF Corporation, NC, USA) have been recommended for use in *Phragmites* control (Mozdzer et al. 2008). The 185 organizations that report using herbicide report targeting a total of 83,000 ha of non-native *Phragmites*. Using the lowest (5% concentration, 2.83 L/acre) and highest (10% concentration, 4.73 L/acre) recommended concentrations of glyphosate, and assuming the respondents treated their acreage 1-5 times over 5 years, we arrive at a range of 28,212—20,000,000 L undiluted glyphosate product applied over the past 5 years. Using the lowest (0.5% concentration, 0.94 L/acre) and highest (5% concentration, 2.83 L/acre) recommended concentration of imazapyr, and assuming the respondents treated their acreage 1-5 times over 5 years, we arrive at a range of 940.5—141,062 L of undiluted imazapyr product applied over the past 5 years. Therefore, we can extrapolate that somewhere between 940—470,000 L of undiluted herbicide product have been applied to approximately 80,400 ha of land in the past five years.

Management goals and ratings of success

Frequently high-rated motivations for *Phragmites* management include “restoration of native plant species,” “improvement of ecosystem function,” and “restoration of native fauna” (Table 2.1). “Restoration of natural hydrology,” “aesthetic reasons,” and “restoration of historical view” received lower ratings, and

Table 2.1: Distribution of participant ratings (percentage and number of total respondents) of organizational reasons for non-native *Phragmites* control. Ratings are on a scale of 1 (strongly disagree) to 5 (strongly agree).

What are the reasons that your organization is attempting to control non-native <i>Phragmites</i>?						
	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response average
Improvement of transportation	7.6% (14)	3.8% (7)	10.3% (19)	23.2% (43)	55.1% (102)	1.85
Improvement of tourism	4.3% (8)	8.6% (16)	14.6% (27)	23.8% (44)	48.6% (90)	1.96
Concern about water availability	7.0% (13)	9.7% (18)	14.5% (27)	22.6% (42)	46.2% (86)	2.09
Restoration of historical view	11.2% (21)	10.1% (19)	26.1% (49)	23.9% (45)	28.7% (54)	2.51
Aesthetic reasons	13.7% (26)	20.5% (39)	24.7% (47)	20.0% (38)	21.1% (40)	2.86
Restoration of natural hydrology	27.0% (51)	24.3% (46)	32.3% (61)	7.4% (14)	9.0% (17)	3.53
Restoration of native fauna	56.5% (109)	17.1% (33)	18.1% (35)	2.6% (5)	5.7% (11)	4.16
Improvement of ecosystem function	70.1% (138)	17.3% (34)	8.1% (16)	2.5% (5)	2.0% (4)	4.51
Restoration of native plant species	77.7% (153)	13.2% (26)	5.1% (10)	0.5% (1)	3.6% (7)	4.61

“concern about water availability,” “improvement of tourism,” and “improvement of transportation” appeared to be of little concern.

Many individuals responded that their organization had been successful at temporary *Phragmites* control; success in long-term *Phragmites* control was more elusive (Table 2.2). Respondents gave high ratings to successful increases in abundance and richness of native plant species, although rated restoration of pre-invasion plant communities as less successful. Few considered *Phragmites* control efforts as successful in increasing the abundance or richness of animal species. Even fewer respondents felt that control efforts had restored pre-invasion hydrology or led to an increase in tourism.

Respondents whose organization had managed *Phragmites* in the past 5 years rate lack of personnel and lack of monetary resources as the most prominent factors constraining *Phragmites* control (Table 2.3), with “lack of data on effective herbicides,” “re-invasion of *Phragmites* after control,” and “the population is not accessible” of intermediate importance. Fewer respondents considered re-invasion of non-native plants after control or lack of data on ecological or economic impacts as impediments of *Phragmites* management. Regulations prohibiting the use of chemical or mechanical control, as well as lack of public support for control efforts, were considered of minimal importance. Of respondents whose organization had not managed *Phragmites* in the past 5 years, many felt that possible *Phragmites* control was constrained by a lack of personnel and a lack of monetary resources (Table 2.4). A number of respondents felt that *Phragmites* is not a high-priority invasive species in the area that they manage. Some respondents stated that *Phragmites* populations are inaccessible or not present on the land they manage. Few respondents felt constrained by regulation prohibiting the use of chemical or mechanical control, or by a lack of data on economic or ecological impacts. Few respondents agreed that there was

concern over non-target effects, a lack of effective herbicides, that past failure to control wetland invasive species constrains *Phragmites* management, that *Phragmites* provides ecosystem services, or that invasive species are not a high priority issue for their organization.

Ordinal logistic regression indicates that none of the sub-questions regarding ratings of success are significantly correlated with hours/ha/yr or dollars/ha/yr spent on *Phragmites* control—in other words, there is no relationship between the amount of money or time spent per hectare on *Phragmites* control and how respondents rate any metric of *Phragmites* management success. There is also no relationship between whether or not herbicide has been used as a control method in the past 5 years and any metric of management success.

Table 2.2: Distribution of participant ratings (percentage and number of total respondents) of non-native *Phragmites* control success. Ratings are on a scale of 1 (strongly disagree) to 5 (strongly agree).

Do you consider that your organization's attempts at non-native <i>Phragmites</i> control have been successful in the following regards:						
	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response average
Increase in tourism	3.3% (6)	4.4% (8)	23.2% (42)	26.5% (48)	42.5% (77)	1.99
Restoration of pre-invasion hydrology	8.6% (16)	17.8% (33)	37.3% (59)	24.3% (45)	11.9% (22)	2.87
Increase in number of native fauna species	9.3% (17)	17.5% (32)	36.6% (67)	27.3% (50)	9.3% (17)	2.90
Increase in abundance of native fauna species	9.3% (17)	17.6% (32)	38.5% (70)	25.8% (47)	8.8% (16)	2.93
Restoration of pre-invasion fauna	8.2% (15)	17.9% (33)	43.5% (80)	22.3% (41)	8.2% (15)	2.96
Long-term control of <i>Phragmites</i> abundance	14.2% (27)	24.7% (47)	24.7% (47)	22.1% (42)	14.2% (27)	3.03
Restoration of pre-invasion plant species	13.1% (25)	30.4% (58)	30.4% (58)	19.4% (37)	6.8% (13)	3.24
Increase in number native plant species	20.6% (39)	24.9% (51)	27.0% (51)	21.2% (40)	6.3% (12)	3.32
Increase in abundance of native plant species	27.9% (53)	22.1% (47)	24.7% (47)	20.0% (38)	5.3% (10)	3.47
Temp control of <i>Phragmites</i> abundance	45.8% (88)	28.1% (21)	10.9% (21)	10.9% (21)	4.2% (8)	4.01

Table 2.3: Distribution of participant ratings (percentage and number of total respondents) of factors that constrain *Phragmites* control (organizations that have managed *Phragmites* in the past 5 years). Ratings are on a scale of 1 (strongly disagree) to 5 (strongly agree).

Do you feel that the following scenarios constrained control of <i>Phragmites</i> on the land that your organization manages?						
	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response average
Regulation prohibiting the use of mechanical control	3.7% (7)	4.2% (8)	14.2% (27)	31.1% (59)	46.8% (89)	1.87
Lack of data on economic impacts	5.2% (10)	16.2% (31)	22.0% (42)	30.9% (59)	25.7% (49)	2.45
Lack of public support for control efforts	10.5% (20)	11.1% (21)	24.7% (47)	30.0% (57)	23.7% (45)	2.55
Regulation prohibiting the use of chemical control	12.0% (23)	15.1% (29)	19.8% (38)	22.9% (44)	30.2% (58)	2.56
Lack of data on ecological impacts	6.3% (12)	18.8% (36)	23.4% (45)	29.2% (56)	22.4% (43)	2.57
Re-invasion of non-native plants after control	7.9% (15)	22.0% (42)	30.9% (59)	26.2% (50)	13.1% (25)	2.85
Population not accessible	20.2% (39)	31.6% (61)	18.7% (36)	14.5% (28)	15.0% (29)	3.27
Re-invasion of <i>Phragmites</i> after control	23.3% (45)	28.5% (55)	28.0% (54)	10.9% (21)	9.3% (18)	3.46
Lack of data on effective herbicides	28.1% (54)	26.6% (51)	22.9% (44)	13.0% (25)	9.4% (18)	3.51
Lack of monetary resources	37.4% (73)	24.6% (48)	17.4% (34)	14.4% (28)	6.2% (12)	3.73
Lack of personnel	43.1% (84)	34.4% (67)	10.8% (21)	7.7% (15)	4.1% (8)	4.05

Table 2.4: Distribution of participant ratings (percentage and number of total respondents) of factors that constrain *Phragmites* control (organizations that have not managed *Phragmites* in the past 5 years). Ratings are on a scale of 1 (strongly disagree) to 5 (strongly agree).

If your organization HAS NOT managed non-native <i>Phragmites</i> in the past 5 years, please indicate why you feel your organization has not undertaken <i>Phragmites</i> management.						
	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response average
Invasive species not a high priority	7.4% (5)	5.9% (4)	7.4% (5)	11.8% (8)	67.6% (46)	1.74
<i>Phragmites</i> provides ecosystem services	1.5% (1)	5.9% (4)	11.8% (8)	26.5% (18)	54.4% (37)	1.74
Past failure to control wetland inv species	7.4% (5)	2.9% (2)	11.8% (8)	29.4% (20)	48.5% (33)	1.91
Regulations prohibiting mechanical control	2.9% (2)	10.3% (7)	13.2% (9)	22.1% (15)	51.5% (35)	1.91
Lack of effective herbicides	4.4% (3)	7.4% (5)	23.5% (16)	23.5% (16)	41.2% (28)	2.10
Concern over non-target effects	2.9% (2)	8.8% (6)	25.0% (17)	25.0% (17)	38.2% (26)	2.13
Lack of data: ecological impacts of <i>Phragmites</i>	2.9% (2)	11.8% (8)	16.2% (11)	33.8% (23)	35.3% (24)	2.13
Lack of data: economic impacts of <i>Phragmites</i>	3.0% (2)	13.6% (9)	21.2% (14)	28.8% (19)	33.3% (22)	2.24
Regulations prohibiting chemical control	13.2% (9)	14.7% (10)	10.3% (7)	19.1% (13)	42.6% (29)	2.37
Population inaccessible	6.0% (4)	11.9% (8)	28.4% (19)	23.9% (16)	29.9% (20)	2.40
<i>Phragmites</i> not a high priority invasive	14.5% (10)	21.7% (15)	15.9% (11)	23.2% (16)	24.6% (17)	2.78
Lack of monetary resources	14.9% (10)	23.9% (16)	26.9% (18)	19.4% (13)	14.9% (10)	3.04
Lack of personnel	23.5% (16)	20.6% (14)	22.1% (15)	20.6% (14)	13.2% (9)	3.21
<i>Phragmites</i> not present	52.2% (47)	8.9% (8)	3.3% (3)	6.7% (6)	28.9% (26)	3.49

Attitudes towards biocontrol

The vast majority (91%, N=260) of respondents are comfortable with the use of a biocontrol agent to manage *Phragmites* populations if the biocontrol agent is specific to non-native *Phragmites* and there appears to be no risk to native *Phragmites*. Only 2% of respondents (N=5) report that they are never comfortable with the use of biocontrol, and only 14% (N=41) indicate that they believe biocontrol should only be an option if chemical, mechanical, and physical measures are unable to stop *Phragmites* invasion. The majority of the respondents (57%, N=162) would accept the use of biocontrol if the agent attacked native *Phragmites* in confinement, but not in the field (65% of those that have managed *Phragmites* in the past 5 years, 40% of those who have not). In total, 46% (N=131) would accept attack of native *Phragmites* in the field, but only if it did not lead to a significant decline (50% of those that have managed *Phragmites* in the past 5 years, 35% of those who have not). A surprisingly high 18% (N=51) of respondents are willing to accept the use of biocontrol even if the agent were to cause a population-level decline of both the non-native and native type (21% of those who have managed *Phragmites* in the past 5 years, 10% of those that have not). There is no geographic pattern to responses (i.e. those who accepted this scenario are not primarily from the East or West), nor are respondents affiliated with any one type of organization more likely to accept a particular scenario. There is no notable difference in any response based upon whether or not respondents have native *Phragmites* on the land that they manage.

Discussion

Our data indicate that there is a large range of resources spent (both in dollars and time) on invasive plant management, and on *Phragmites* management in particular. Despite a total expenditure of anywhere from less than \$1 to \$800,000 per

year on *Phragmites* control (sum=\$4.6 million), most organizations do not rate themselves as successful in achieving a number of management goals, such as long-term control of *Phragmites* or restoration of native plant communities. Respondents state that their organizations are most-often constrained by a lack of personnel and lack of monetary resources. However, there is no relationship between the amount of money or time spent per hectare on *Phragmites* control and any metric of perceived management success. There was also no correlation between any one type of control method and perceived management success. The results suggest that despite high expenditure in money, time, and chemicals, many managers feel that their organization has not been successful at meeting the goals of *Phragmites* management.

The results of this survey also highlight an alarming trend towards using herbicide as a primary method of invasive plant control, with little evidence that such control is effective. Federal, state, land trust, and private land managers that participated in this survey are responsible for treating 83,000 ha of wetland habitat with somewhere between 28,000-20,000,000 L of active herbicide product over the past five years. Aerial or ground spraying of herbicide or pesticide to control non-native species is a common practice (Reid et al. 2009) that is not confined to *Phragmites* management. Compounds such as imazapyr and glyphosate are also used for the control of other non-native plant species in natural areas, such as *Lythrum salicaria*, *Arundo donax*, *Cephalanthus occidentalis*, *Melaleuca quinquenervia*, *Panicum repens*, *Setaria magna*, *Tamarix* spp., *Typha* spp., *Alliaria petiolata*, *Hieracium aurantiacum*, *Frangula alnus*, *Pueraria lobata*, *Wedelia texana*, *Rosa multiflora*, *Scaevola* spp., and *Schinus terebinthifolius* (to name a few). Of the \$6.3 billion spent in the US on herbicide in 2000, \$1.36 billion was spent for non-agricultural use. Individuals and organizations used 110 million lbs of herbicide to target undesired plant species in non-agricultural areas (Kiely et al. 2004). No data

exist as to what percentage of this expenditure is incurred by conservation organizations. Extrapolating an average cost of \$12.36/lb herbicide, the 2006 cross-agency budget for invasive species management of \$491 million could have been used to purchase a total of 39.7 million lbs of herbicide. Obviously, the federal invasive species control budget was put towards other control methods as well—yet the point remains that public and private organizations charged with land stewardship are releasing an unknown (large) amount of herbicide into the environment.

There is currently little evidence that herbicide provides for long-term, sustainable control of invasive plants. In our results, Only 8 of 68 managers felt that *Phragmites* management is constrained by the non-target impacts of herbicide use. Although herbicides such as glyphosate have been lauded as having “very low toxicity to wildlife” (Monsanto 2005), an increasing body of literature demonstrates that glyphosate is more mobile and is more pervasive in the environment than previously claimed (Thurman and Cromwell 2000, Baker et al. 2006, Scribner et al. 2007, Battaglin et al. 2009). The reported half-lives of glyphosate and imazapyr in soil are 60 and 64-143 days respectively (US EPA 2010). Herbicide application has been documented to decrease populations of threatened native plants while not impacting non-native plant abundance in Montana (Rinella et al. 2009), Australia (Matarczyk et al. 2002), and Minnesota (Blossey et al. 2001). Herbicides and pesticides not only affect native plant survival—they can directly harm non-target organisms, a phenomenon that is amplified up the food chain (Innes and Barker 1999, Cauble and Wagner 2005, Relyea 2005, Hayes et al. 2010). Land managers, scientists, and the public rarely consider these serious and documentable effects of invasive plant control.

The use of chemical control is particularly questionable when there are few efforts to collect data before, during, and after management in order to evaluate

management outcomes (Blossey 1999). Even without access to quantitative data, the participants in our survey gave mid-range to low ratings to most management success metrics. Previous studies that have analyzed quantitative data on the effects of invasive plant management suggest that there are rarely observable benefits of control programs (Reid et al. 2009, Kovalenk et al. 2010). This lack of management success is partially due to a lack of well-articulated management objectives. The respondents of this survey rated restoration of ecosystem processes and native plant communities as main goals of *Phragmites* management. Thus far, a lack of a uniform definition of “ecosystem harm” has impeded invasive species decision-making (Parker et al. 1994). There needs to be serious discussion in and between the scientific and management communities about what we are managing our natural areas for—specific ecosystem processes, beauty, tourism, historical integrity, species-specific habitat, or some combination of these functions? Without quantifiable objectives and subsequent collection of quantitative data, it is impossible to rate management success.

Chemical control is never the only available invasive plant management option. Invasive plant management could be advanced by focusing on the invaded ecosystem rather than the invader, incorporating restoration measures into management such as native re-seeding or restoration of natural hydrology. There may be positive ecosystem impacts of partial reduction rather than complete eradication of an invader. The results of our survey indicate that few respondents are opposed to the use of biocontrol to manage *Phragmites*—although many managers are concerned about hypothetical impacts to native *Phragmites*. Although the use of biocontrol is sometimes considered “risky” (Simberloff and Stiling 1996), the risks must be weighed against the risk of other management options—such as the non-target impacts of herbicide use, the disturbance created by mowing or disking, and the cost of doing nothing.

The results of this survey highlight the need for better documentation of the entire invasive plant management process: from goal-setting, to implementation and expenditure, to outcomes and success. We also call for greater transparency by public and private land management organizations when using herbicides that may affect ecosystem health beyond the borders of the management area, and that may be ultimately unsuccessful at their intended purpose. It is questionable whether current approaches to *Phragmites* management are efficient, sustainable, or beneficial to native ecosystems. With a more comprehensive understanding of invasive species management, we hopefully can arrive at a more ecologically- and economically-desirable approach to land stewardship.

APPENDIX

***Phragmites australis* invasion and management**

Phragmites australis, a clonal wetland plant, has occurred in North America for at least 40,000 years (Hansen 1978), and paleo-ecological studies indicate that it has been present along the Atlantic and Pacific coasts for several thousand years (Niering 1977, Orson 1999). In the late 1800s, non-native types were introduced to the East Coast from Eurasia (Saltonstall 2002), from where the species spread across much of the continent, overtaking large expanses of wetlands from coast to coast. Public and private organizations have used chemical (herbicide), mechanical (mowing, disking) and physical (flooding, burning) methods in attempt to control invasive *Phragmites* (Marks et al. 1994). Failure to achieve long-term suppression has led researchers to propose alternative control methods, such as planting desired native plant species (Wang et al. 2006) or the use of herbivorous insects (biocontrol) (Tewksbury *et al.* 2002).

North American *Phragmites* management is complicated by the fact that (1) habitats and ranges of native and non-native *Phragmites* overlap, (2) there are conflicting data on ecological impacts of non-native *Phragmites* invasion, and (3) there are currently no effective methods of long-term control. Because scientists and managers could not reliably distinguish native and non-native populations before 2002, we know little about the ecology of native *Phragmites*. There is strong evidence for significant trait variation among *Phragmites* populations (e.g. Hansen et al. 2007, Saltonstall and Stevenson 2007, Park and Blossey 2008, Mozdzer and Zieman 2010). It appears that variation among native or non-native populations is often as-great or greater than overall variation among populations based on their native/non-native origin—in other words, there are highly significant ecological differences among

Phragmites populations, but these differences cannot always be predicted by native or non-native status.

Investigations of *Phragmites* invasion do not point to clear ecosystem impacts. Geographic and biotic context is crucial to determining whether *Phragmites* is ecologically-distinct from a native reference community (e.g. Rooth and Stevenson 2000, Leonard et al. 2002, Silliman and Bertness 2004, Buchsbaum et al. 2006, Lavoie et al. 2003, Hjalten 1991, Hanson et al. 2002, Litvin and Weinstein 2004, Able and Hagan 2000, Grothues and Able 2003). For example, while some research indicates that *Phragmites* invasion affects invertebrate community assemblage (Angradi et al. 2001, Talley and Levin 2001, Robertson and Weis 2005, Park and Blossey 2008), other studies suggest that some or many invertebrate taxa are unaffected (Fell et al. 1998, Rilling et al. 1999, Warren et al. 2001, Gratton and Denno 2005). Such considerations spurred Hershner and Havens (2008) to suggest that non-native *Phragmites* should not be controlled in all circumstances, arguing that the species may provide some positive ecosystem services such as sediment stabilization. Regardless of often-conflicting ecological data, many land management organizations have decided to attempt to prevent the establishment of *Phragmites* monocultures.

Evaluating current and future methods of *Phragmites australis* control Survey instrument

BACKGROUND INFORMATION

Phragmites australis (common reed) is a wetland plant found throughout the Northern hemisphere. In the United States there are two “types” of *Phragmites*

australis: a native type (*Phragmites australis* subsp. *americanus*) and an introduced type.

A non-native *Phragmites* type was introduced from Eurasia to the East Coast of the United States in the mid-nineteenth century. Since its introduction, non-native *Phragmites* populations have expanded across the United States and Canada. Records indicate that many native *Phragmites* populations have declined, particularly in the East and along the Atlantic Coast, whereas in the West and Southwest populations appear stable at the present time.



***Phragmites australis* (common reed)**

Land managers have approached *Phragmites* control using a variety of methods, including local or aerial spray of herbicide, controlled flooding, mowing, disking, or fire. After decades of attempts to control *Phragmites* along the East coast, managers began to explore options for biological control of *Phragmites*. In 1998 the exploratory search for biocontrol agents began in Europe (with the help of CABI Europe, Switzerland Centre). Through work spanning the past decade, several promising control agents have been identified and are currently being studied for their host specificity (see www.invasiveplants.net for an update on biocontrol efforts and a list of recent publications).

SURVEY INSTRUCTIONS

Please complete the following survey in reference to the **local** area that you manage, not the overall holdings of your organization (for example, if you manage a region for the New York Department of Transportation, please answer for that region and not the overall NYDOT).

The survey should take about 15-30 minutes to complete.

DEFINITIONS

Plant biocontrol agent: The release of natural enemies (insects, pathogens) from the home range of an introduced plant in an attempt to reduce populations of the introduced species

Species richness: The total number of different species that exist in a given area

Species abundance: The total number of individuals of a species in a given area

SURVEY

A. In which land category do you primarily work?

- State owned land
- Land-trust owned land
- Privately owned land
- Federally owned land
- Ranch / farm land
- City / municipal owned land
- Employee of academic organization
- Other

B. How many acres, in total, are you involved in managing? _____

C. In what state are you located? [state]

D. In what state county are you located? [county]

E. Approximately how many acres of **native** *Phragmites* are on the land you manage?

F. Has your organization managed **native** *Phragmites* in the past 5 years?

- yes
- no

G. Approximately how many acres of **non-native** *Phragmites* are on the land you manage? _____

D. Has your organization managed **non-native** *Phragmites* in the past 5 years?

- yes
- no

[IF you answered “no” to D, please proceed to question O]

E. What method(s) do you use to control **non-native** *Phragmites*? (check all that apply)

- Chemical (herbicide)
- Mowing / cutting
- Burning
- Removal by hand
- Flooding
- Disking
- Other

G. What is/are the reasons that your organization is attempting to control non-native *Phragmites*?:

[1=strongly disagree 2=somewhat disagree 3=not sure 4=somewhat agree 5=strongly agree]

Improvement of ecosystem function	1.....2.....3.....4.....5
Restoration of native plant species	1.....2.....3.....4.....5
Restoration of native fauna	1.....2.....3.....4.....5
Restoration of natural hydrology	1.....2.....3.....4.....5
Aesthetic reasons	1.....2.....3.....4.....5
Restoration of historical view	1.....2.....3.....4.....5
Improvement in tourism	1.....2.....3.....4.....5
Improvement in transportation	1.....2.....3.....4.....5
Concern about water availability	1.....2.....3.....4.....5

H. Please estimate, to your best knowledge, the total number of **hours** (including travel) your organization has dedicated to **non-native** *Phragmites* control in the **past 5 years**: _____

I. Please estimate, to your best knowledge, the total **dollars** your organization has dedicated to **non-native** *P. australis* control in the **past 5 years**: _____

J. Please estimate, to your best knowledge, the total number of **hours** (including travel) your organization has dedicated to **overall invasive plant control** in the **past 5 years**: _____

K. Please estimate, to your best knowledge, the total **dollars** your organization has dedicated to **overall invasive plant control** in the **past 5 years**: _____

L. Approximately what percent of your organization's **overall plant management budget** (plant material/ planting/ mowing/ plant resource management) has been spent on ***Phragmites* control** in the past 5 years? _____ %

M. Do you consider that your organization's attempts at non-native *Phragmites* control have been successful in the following regards:

[1=strongly disagree 2=somewhat disagree 3=not sure 4=somewhat agree 5=strongly agree]

Temporary control of <i>Phragmites</i> abundance	1.....2.....3.....4.....5
Long-term control of <i>Phragmites</i> abundance	1.....2.....3.....4.....5
Restoration of pre-invasion plant species	1.....2.....3.....4.....5
Restoration of pre-invasion fauna	1.....2.....3.....4.....5
Restoration of pre-invasion hydrology	1.....2.....3.....4.....5
Increase in the number of native plant species	1.....2.....3.....4.....5
Increase in the abundance of native plant species	1.....2.....3.....4.....5
Increase in the number of native faunal species	1.....2.....3.....4.....5
Increase in the abundance of native faunal species	1.....2.....3.....4.....5
Increase in tourism	1.....2.....3.....4.....5

N. Do you feel that the following scenarios constrained control of *P. australis* on the land that your organization manages?

[1=strongly disagree 2=somewhat disagree 3=not sure 4=somewhat agree 5=strongly agree]

Lack of monetary resources	1.....2.....3.....4.....5
Lack of personnel	1.....2.....3.....4.....5
Lack of effective herbicides	1.....2.....3.....4.....5
Lack of data on ecological impacts	1.....2.....3.....4.....5
Lack of data on economic impacts	1.....2.....3.....4.....5
Lack of accessibility (population(s) are difficult to get to)	1.....2.....3.....4.....5
Regulation prohibiting the use of chemical control	1.....2.....3.....4.....5

Regulation prohibiting the use of mechanical control	1.....2.....3.....4.....5
Re-invasion of <i>Phragmites</i> after control	1.....2.....3.....4.....5
Re-invasion of non-native species after control	1.....2.....3.....4.....5
Lack of public support for control efforts	1.....2.....3.....4.....5

O. If your organization has **not** managed non-native *Phragmites* in the past 5 years, please indicate why you feel your organization has not undertaken *Phragmites* management:

[1=strongly disagree 2=somewhat disagree 3=not sure 4=somewhat agree 5=strongly agree]

Phragmites is not present on the land that we manage

1.....2.....3.....4.....5

Phragmites is not a high priority invasive species for our organization

1.....2.....3.....4.....5

Invasive plant species are not a high priority concern for our organization

1.....2.....3.....4.....5

Lack of monetary resources

1.....2.....3.....4.....5

Lack of personnel

1.....2.....3.....4.....5

Past failure to control *Phragmites* or other wetland invasive species

1.....2.....3.....4.....5

Phragmites provides services such as duck blinds, improved water quality

1.....2.....3.....4.....5

Concern over non-target effects (effects of control on other species)

1.....2.....3.....4.....5

Lack of effective herbicides

1.....2.....3.....4.....5

Lack of data on ecological impacts

1.....2.....3.....4.....5

Lack of data on economic impacts

1.....2.....3.....4.....5

Regulations prohibiting the use of mechanical control

1.....2.....3.....4.....5

Regulations prohibiting the use of chemical control

1.....2.....3.....4.....5

Inaccessibility (difficult to access *Phragmites* population(s))

1.....2.....3.....4.....5

P. Please rate your concern about *Phragmites* spread in relation to other introduced plant species on a scale of 1 (lowest) to 5 (highest) (circle one):

1

2

3

4

5

Q. Approximately what percent of your organization's **overall budget** has been spent on **overall invasive plant management** in the past 5 years? _____%

R. Please finish the following sentence, checking **all** statements that you agree with:
"I would be comfortable with the use of a biocontrol agent to control Phragmites... _____"

- ... never; I am not comfortable with the use of biocontrol.
- ... only if chemical, mechanical, and physical measures are unable to stop the invasion of non-native Phragmites.
- ... if the biocontrol agent is specific to non-native Phragmites and there appears to be no risk to native Phragmites.
- ... if the biocontrol agent will attack non-native and native Phragmites genotypes in confinement, but only the non-native genotype in the field.
- ... if the biocontrol agent will attack both non-native and native Phragmites in the field, but only leads to significant decline of non-native Phragmites.
- ... if the biocontrol agent will attack both non-native and native Phragmites in the field, leading to a population level decline in both non-native and native Phragmites.

S. The final six questions are hypothetical questions, but your response will be used to better understand trade-offs that people make when considering purchase of land for conservation. Please read all options carefully and answer realistically, remembering that resources are limited and your organization has other expenses. Please treat each question separately, even if options appear similar.

1. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 50 acres – 10% invaded by Phragmites - 1 rare species - \$8000 per acre
- 5 acres - 70% invaded by Phragmites - 10 rare species - \$10,000 per acre
- 500 acres - 50% invaded by Phragmites - 20 rare species - \$4000 per acre

2. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 500 acres - 70% invaded by Phragmites - 10 rare species - \$4000 per acre
- 50 acres – 50% invaded by Phragmites - 20 rare species - \$2000 per acre
- 100 acres – 1% invaded by Phragmites - 5 rare species - \$10,000 per acre

3. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 500 acres - 70% invaded by Phragmites - 1 rare species - \$2000 per acre
- 100 acres - 50% invaded by Phragmites - 10 rare species - \$10,000 per acre
- 50 acres - 1% invaded by Phragmites - 5 rare species - \$4000 per acre

4. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 5 acres - 1% invaded by Phragmites – 5 rare species - \$8000 per acre
- 10 acres – 10% invaded by Phragmites - 10 rare species - \$2000 per acre
- 100 acres - 50% invaded by Phragmites - 1 rare species - \$4000 per acre

5. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 500 acres - 50% invaded by Phragmites - 10 rare species - \$4000 per acre
- 100 acres - 1% invaded by Phragmites - 20 rare species - \$2000 per acre
- 50 acres - 70% invaded by Phragmites - 5 rare species - \$8000 per acre

6. Your organization has the ability to purchase a new parcel of land. Which would you chose from the following three options? (pick one)

- 50 acres - 70% invaded by Phragmites - 1 rare species - \$10,000 per acre
- 5 acres - 50% invaded by Phragmites - 5 rare species - \$2000 per acre
- 100 acres - 10% invaded by Phragmites - 10 rare species - \$4000 per acre

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CHAPTER 3

ECONOMIC IMPACT OF NON-NATIVE PLANTS IN TERMS OF TRADE-OFFS

Abstract

Although invasive species are defined by U.S. law as species that cause environmental or economic harm, we have a limited understanding of each concept. In this paper, we use conjoint analysis, a method of non-market valuation, to explore the economic impact of non-native plant species. We received responses from 285 land-managers that are involved in management of 12% of the continental United States. Our results describe the cost of invasive species in terms of tradeoffs relevant to the acquisition of conservation land: percent non-native plant cover, number of rare plant species, acreage, and annual cost of management. We find that the presence of non-native plant species has a discernable effect on individual utility (satisfaction), as do other land attributes such as the presence of rare plant species and acreage. Our data support previous studies that suggest a significant economic impact of invasive species, while simultaneously modeling the effect of other land attributes on land parcel desirability.

Introduction

An invasive species, as defined by U.S. Executive Order 13112, is a non-native species whose introduction does or is likely to cause “environmental harm” or “economic harm.” Defining environmental harm has proven difficult (Richardson and van Wilgen 2004, Sagoff 2005); an understanding of economic harm has proven even more elusive due to a “dearth” of literature on the subject (Barbier 2001, Shogren 2005).

At present there are well over 4,300 known non-native species in the United States (US OTA 1993). Non-native species have been charged with altering nutrient cycling, plant productivity, abiotic site conditions, human health, and native biodiversity (Mack et al. 2000, Mooney and Hobbs 2000)—in fact, invasive species are considered the second greatest threat to imperiled species in the United States (Wilcove et al. 1998). These ecosystem changes can impact economic values that are captured by markets, such as the cost of decreased livestock production (Leitch et al. 1994). Less obviously, invasive species can also affect values that are not captured by economic markets.

Environmental economists use the idea of total economic value (TEV) to describe the combined value of all ecosystem functions. The TEV of an ecosystem not only includes values captured by markets (direct values), but also values that are not captured by markets such as recreation and existence values. Invasive species can impact both market and non-market values of an ecosystem. For example, consider a forest that is invaded by kudzu (*Pueraria lobata*). The proliferation of this weedy vine could affect marketable timber production; it could also affect tourism revenue, if the forest is a visitor destination. The invasion may also affect the “existence value” of the forest, or the benefit that an individual receives from knowing that a particular environmental resource exists in a certain state. As outlined in Figure 1, an invasive species could impact many of the values that comprise the TEV of an ecosystem. Over the past twenty years, these impacts to ecosystem TEV have lead land stewards to actively control against the proliferation of non-native species.

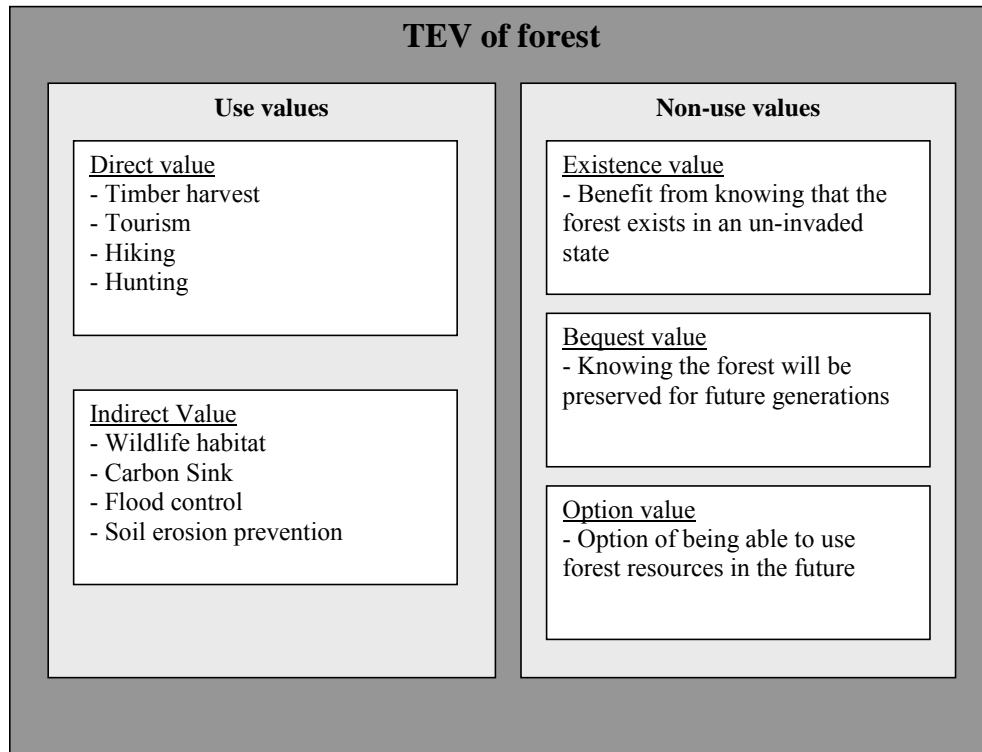


Figure 3.1. Hypothetical components of the Total Economic Value (TEV) of a forest impacted by Kudzu invasion.

The impact of invasive species on ecosystem use-values has been investigated through bioeconomic modeling (Settle and Shogren et al. 2006), travel-cost methods (Nunes et al. 2004), hedonic property value methods (Holmes et al. 2006, Earnhart 2001), documentation of land abandonment (Schneider and Geogehan 2006), recreational losses (Eiswerth et al. 2005), and most commonly, market impacts of single species (for review, see Born et al 2005, Lovell et al 2006, Olson 2006). Impacts to non-use value are less-frequently studied, but have recently been explored in the context of marsh restoration in Connecticut (combined discrete-choice hedonic analysis and choice-based conjoint analysis, Earnhart 2001), a marine protection program in the Netherlands (travel-cost and contingent valuation, Nunes et al. 2004), and invasive plant control in U.S. National Forests (dichotomous-choice with and

without an “unsure” option, Champ et al. 2005). Most recently, McIntosh et al. (2010) surveyed U.S. households, finding that the average respondent was willing to make a one-time payment of \$34 to delay “low impacts” of aquatic invaders for one year, \$48 to delay “high impacts” for one year, and \$218 to delay “high impacts” for a decade.

In this paper we use conjoint analysis, a method of non-market valuation, to analyze how U.S. land-managers make tradeoffs between the acreage, number of rare species, percent cover of invasive plant species, and cost of management of various land parcels. Conjoint analysis is a stated preference method that is used to determine how people value different features or attributes that make up a good or service. The method is based upon the consumer theory developed by Lancaster (1966, 1991), which assumes that economic utility (a measure of relative satisfaction) is derived from the individual attributes of goods. The overall utility of a good can therefore be decomposed into separate utilities for each of its attributes (Louviere 1994). This is particularly useful for valuing environmental entities such as ecosystems that consist of multiple attributes. From these utilities one can calculate marginal values—the effect of adding one more unit of a good on individual utility, as well as marginal rates of substitution—the rate at which a consumer is ready to give up one good in exchange for another good while maintaining the same level of satisfaction.

Data for conjoint analysis is generated experimentally. Respondents are given a survey in which they are asked to choose from, rank or rate hypothetical goods (profiles) that are composed of multiple levels of multiple attributes. Respondents are presented with a choice among a set of profiles. In subsequent questions, the respondent will choose within other sets of profiles that vary in the levels of each attribute. An orthogonal fractional factorial design is used to reduce the number of overall profiles that a respondent must evaluate. This design allows the researcher to test for main effects but not interactions (Holmes and Adamowicz 2003).

Conjoint analysis has been increasingly applied to the environmental management issues that involve tradeoffs not represented in market transactions, such as values for protecting threatened caribou populations (Adamowicz et al 1998), preferences for waterfowl hunting (MacKenzie 1993), watershed quality improvements (Farber and Griner 2000), and community forest contracts (Arifin et al. 2009). Such stated preference methods have both advantages and drawbacks. A hypothetical choice setting mimics real choice settings by requiring the individual to simultaneously consider multiple dimensions of alternatives. The researcher is able to infer tradeoffs between attributes, as well as the marginal values of specified levels of attributes. However, stated preference methods are commonly critiqued because of the hypothetical nature of the questions and the fact that actual behavior is not observed (Cummings et al. 1986, Mitchell and Carson 1989, Arrow et al. 1993). Nevertheless, stated preference methods are currently the only option for measuring non-use values, and they are frequently used to study valuation in cases that involve a change in environmental quality.

Methods

Survey

The conjoint question was embedded within a larger survey on management of a common wetland invasive species, *Phragmites australis* (Martin Chapter 2). We conducted an online survey of land managers working for federal (e.g. Fish and Wildlife Service, National Park Service, Army Corps of Engineers), state (e.g. departments of environment, natural resources, agriculture, and transportation), municipal, land-trust (e.g. The Nature Conservancy) and other private organizations (e.g. Ducks Unlimited, consultants) (available from the authors upon request). We sent email solicitations to approximately 500 individuals who had previously expressed

interest in *Phragmites* management, as well as professional list-servs (e.g. Ecological Society of America, invasive plant groups), asking recipients to forward the solicitation email to any appropriate colleagues. We tested a draft survey in a number of pilot interviews with NY state and federal land managers; a modified draft was presented to a focus group of private and public land managers in April 2009. We disseminated the final version online in October 2009.

Respondents were asked background questions on their affiliation (federal, state, or private organization), the amount of land they are involved in managing, and their organization's invasive plant management budget. Respondents were then presented with six questions in which they were asked to choose between three parcels of land that varied in the levels of four attributes: acreage (10,50, 100 or 200 acres), percent non-native plant cover (1, 10, 50, or 70 % cover), number of rare plant species (1, 5, 10 or 20 species), and cost of management per acre (\$1000, \$3000, \$5000, or \$10000 /acre) (Table 3.1). Respondents were told that although the questions are hypothetical, their responses will be used to better understand trade-offs that managers make when considering conservation land parcels. Respondents were asked to read all options carefully, treating each question separately even if options appeared similar, and to answer realistically, remembering that resources are limited and his or her organization has other expenses. The number of profiles was reduced to a manageable size (N=54 profiles) using an orthogonal fractional factorial design (SPSS Inc., Chicago IL) that treated all attributes as independent and precluded collinearity between them in an empirical model (Mackenzie 1993). The respondents were randomly stratified into three pools (Holmes and Adamowicz 2003), each of which was presented with six sets of three profiles.

Table 3.1: An example of a land attribute choice-set included in the survey

Your organization has the ability to purchase a new parcel of land. Which would you choose from the following three options?					
	Acres	Percent non-native plant cover	No. of rare species	Cost of management per acre	Choice
Option 1	10	1 %	5	\$ 5000	<input type="checkbox"/>
Option 2	10	70 %	5	\$ 3000	<input type="checkbox"/>
Option 3	100	10 %	10	\$ 5000	<input type="checkbox"/>

Conjoint approach

We begin with the assumption that land managers derive utility from the attributes of conservation land parcels. Based on the random utility model of McFadden (1974), the manager i 's utility of choosing option j is defined by

$$U_{ij} = V_{ij} + \varepsilon_{ij}$$

where V_{ij} is the deterministic indirect utility function and ε_{ij} is a stochastic portion. V_{ij} is assumed as a linear function of acreage, non-native plant cover, number of rare plant species, and cost of management per acre, and can be expressed as:

$V_{ij} = \beta_1 \text{ acreage} + \beta_2 \text{ non-native cover} + \beta_3 \text{ rare plant spp} + \beta_4 \text{ cost of management}$
 where β_n is the marginal utility for the n th attribute.

Logit model

Data from the 285 respondents were analyzed using the choice modeling platform in JMP 8.0 (SAS Institute Inc., Cary NC). The variables acreage, percent non-native plant cover, number of rare plant species, cost of management per acre, and interactions between respondent affiliation and these variables were included in the

fitting of the discrete choice data to a multinomial logit model using a variation of Firth bias-adjusted maximum likelihood estimation (Firth 1993).

Assuming that the stochastic component is an independently distributed value, the standard multinomial logit model (MNL) yields the probability of individual i choosing alternative j , outlined as:

$$\text{Prob}(j \text{ is chosen}) = \frac{e^{V_{ij}}}{\sum_{k=1}^J e^{V_{ik}}}$$

We also tested for significant interactions between respondent affiliation and these variables. Here we report the results of the multinomial logit model with the best AICc and Firth LogLikelihood values.

Results

Participants

It is impossible to calculate the exact response rate because we do not know the final number of recipients, but we believe the 285 collected responses represent a significant proportion of land managers across the United States. A response rate can be approximated through descriptive statistics. Surveys were returned from land managers in 40 states (states not included = AK, AR, CO, HI, LA, MO, MS, NM, OK, WV), representing 425 counties. In total, the 285 land managers that participated in the survey are responsible for the management of approximately 200 million acres, or 12.3% of the area of the continental United States (Table 3.2). This number may seem high, but the federal government alone owns approximately 21.4% of the area in the continental United States. The organizations captured in this survey spend a combined

total of approximately \$35 million per year on the management of invasive plant species (Martin Chapter 2). In comparison, the U.S. federal budget for overall invasive species control was reported at \$466 million in 2006 (US NISC 2006).

Table 3.2: Summary of respondent information

Type of organization	Responses	States Represent.	Counties Represent.	Max acres managed	Total acres managed
State	65	20	144	315,800	11,369,320
Private	111	32	130	55,643,520	134,685,786
Land trust	18	9	32	275,000	386,390
Federal	67	31	93	43,962,966	53,880,029
Municipal	24	9	26	26,000	100,150
Total	285	40	425		200,421,675

Conjoint analysis

The estimates of the MNL model for each land attribute are presented in Table 3.3. The null hypothesis that all parameters are zero is rejected by the likelihood ratio test ($P < 0.0001$). The attribute “number of rare plants” had the strongest impact on manager’s choices ($\beta = 0.0627$), followed by percent cover of non-native plants ($\beta = -0.0190$), number of acres ($\beta = 0.00697$), and cost of management per acre ($\beta = -0.000172$). Unsurprisingly, number of rare plants and acreage had positive coefficients across the three respondent affiliations (public, private, state), whereas percent cover of non-native plants and cost of management per acre had negative coefficients.

There are significant interactions between respondent affiliation and percent cover of non-native plants, as well as affiliation and cost of management per acre. Percent cover of non-native plants most affects state manager utility ($\beta = -0.00611$),

followed by private ($\beta=0.00267$) and federal managers ($\beta=0.00344$). Cost of management per acre most affects state managers ($\beta=-0.0000541$), followed by private ($\beta=-0.0000128$) and federal managers ($\beta=0.0000669$). In other words, marginal increases in non-native plants or cost of management are more likely to impact the choices of state managers than private or federal managers.

Rather than place an absolute dollar value on a non-market impact, this survey relates invasion impact to currency that is relevant to land-managers: marginal rate of substitution between land attributes. Treating federal, state, and private managers as one group, the results of this survey suggest that a 1% increase in non-native plant cover affects individual utility as much as a \$100.64/acre increase in cost of management, or a 2.73 acre reduction in acreage (Table 3.4). Meanwhile, an increase of 1 rare plant species is equivalent to a \$364.65/acre reduction in cost of management, or a 9.01 acre increase in land area. These numbers are reasonably scaled in relation to the budgets and scales that land management agencies experience.

As a linear model, our results are limited by the fact that they do not reflect a diminishing effect of increasing non-native plant cover—in other words, it seems unlikely that an increase from 0% to 10% non-native plant cover would have the same value as an increase from 80% to 90% percent cover. It is likely that the model is more accurate at lower levels of percent invasion—although to our knowledge, no researchers have explored whether there is a threshold of invasion at which the marginal value of invasion decreases.

Table 3.3: Multinomial logit model estimates for the choice experiment.

Variable	Coefficient	Std error
Acres	0.0069653	0.0004834
% cover of non-native plants	-0.0190407	0.0014647
Number of rare plants	0.0627556	0.0057135
Cost of management per acre	-0.0001721	0.0000115
Federal*Acres	0.0000637	0.0007054
Private*Acres	0.0001600	0.0005985
State*Acres	-0.0002238	0.0006519
Federal*% cover of non-native plants	0.0034395	0.0021205
Private*% cover of non-native plants	0.0026668	0.0017981
State*% cover of non-native plants	-0.0061063	0.0019593
Federal*Number of rare plants	0.0051738	0.0083107
Private*Number of rare plants	-0.0025157	0.0070891
State*Number of rare plants	-0.0026581	0.0019593
Federal*Cost of management per acre	0.0000669	0.0000166
Private*Cost of management per acre	-0.0000128	0.0000143
State*Cost of management per acre	-0.0000541	0.0000155

Bold denotes values that are statistically significant (effect likelihood ratio tests, $P \leq 0.05$)

Table 3.4: Marginal rates of substitution of non-native plant cover and number of rare plants (in +/- cost of management per year and in +/- acres) by type of organization. “Full model” indicates the marginal rates of substitutions when state, federal, and private organizations are treated as one data set.

Type of organization	1% increase in non-native plant cover	+ 1 increase in number of rare plants
State	\$111.17/acre -3.73 acres	-\$265.68/acre 8.91 acres
Federal	\$148.30/acre -2.22 acres	-\$645.72/acre 9.66 acres
Private	\$88.56/acre -2.30 acres	-\$325.80/acre 9.53 acres
Full model	\$110.64/acre -2.73 acres	-\$364.65/acre 9.01 acres

Discussion

The results of this survey suggest that even small increases in non-native plant cover have a substantial affect on individual utility. An application of this type of analysis to a larger group of stakeholders—i.e. to the general public rather than land managers—would further elucidate the economic impact of invasive species. Thus far, those attempting to assess the impact of invasive species at a national scale have arrived at numbers between \$128 billion (Pimentel 2005) and \$185 billion (US OTA 1993). However, these estimates were calculated using a damage-function approach, in which the invasive species is assumed to impose costs without contributing any benefits (Freeman 1993, Perrings et al. 2000, Knowler and Berbier 2005) These estimates are also upwardly-biased because they are based upon constant marginal damage per species, constant control costs, and market prices for affected products (Olson 2006, Shogren et al. 2006). Non-market valuation techniques, such as conjoint analysis, may provide a better alternative for estimating the economic impact of non-native species.

Species invasion does not occur within a vacuum—the conservation value of a land parcel is dependent on the state of multiple attributes. Our results suggest that the introduction of one rare plant species has a greater impact on individual utility than a 1% reduction in invasive plant cover. Stated another way, managers perceive that the addition of 1 rare plant species has the same benefit as a 3.3% reduction to invasive plant cover, a 9.01 acre increase to land holdings, or a decrease of \$364.65/acre in management costs. In another example, suppose that a conservation organization is successful in a 50% decrease in non-native plant cover. Our results suggest that U.S. land managers would value a 50% reduction in non-native plant cover the same as a

\$5032/acre decrease to cost of management, an addition of 136.5 acres, or the addition of 15 rare plant species.

At the present time, many natural area management programs focus on the invader rather than the invaded ecosystem (Hobbs and Humphries 1995)—yet ultimately, it will be impossible to control the more than 4,300 non-native species found in the United States (US OTA 1993). Previous surveys of land managers in Australia (Reid et al. 2009) and the northeastern U.S. (Acharya 2009) suggest that eradication of target non-native species is rarely accomplished. Our results suggest that substantial gains in utility can be made without the complete eradication of non-native plant cover. It is often taken for granted that non-native plant control is equivalent to native plant protection, but this is rarely the case (Smith et al. 2006). Restoration activities that reduce but do not eliminate non-native species may have a positive impact on utility, as would planting rare species. The resources available to conservation organizations are limited (Barnett et al. 2007; Bergstrom et al. 2009), and the decision to allocate resources towards non-native plant management inherently takes resources away from other forms of management. Understanding plant invasion in the language of management trade-offs can help us to develop a more holistic approach to land management.

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