Conservation While Under Invasion: Insights from a rare Hemiparasitic Plant, Swamp Lousewort (Pedicularis lanceolata Michx.)

CONSERVATION WHILE UNDER INVASION: INSIGHTS FROM A RARE HEMIPARASITIC PLANT, SWAMP LOUSEWORT (*Pedicularis lanceolata* Michx.)

A Dissertation Presented

by

SYDNE RECORD

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CONSERVATION WHILE UNDER INVASION:
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DEDICATION

To Noah and Annie.

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ABSTRACT

CONSERVATION WHILE UNDER INVASION: INSIGHTS FROM A RARE HEMIPARASITIC PLANT, SWAMP LOUSEWORT (*Pedicularis lanceolata* Michx.)

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Competition with non-native invasive species is considered a major threat to many rare native species. As such, invasives removals are a common management strategy. Rare native species that interact uniquely with other organisms in their community (*e.g.*, hemiparasitic plants) may be adversely affected by removing invasives. A management plan for a regionally rare hemiparasitic plant in Massachusetts, *Pedicularis lanceolata* Michx., identified invasives as a threat, but more quantitative evidence is needed to determine how *P. lanceolata*'s persistence is influenced by its co-occurrence with native or invasive hosts. This research asks how *P. lanceolata* is affected by growth with native versus invasive hosts. Chapter I describes the species associated with *P. lanceolata* throughout its range, comparing areas where it is considered common and rare. Relative abundances of natives, non-native invasives, non-native non-invasives, and species with both native and non-native genotypes growing with *P. lanceolata* did not differ significantly at sites where the species is considered common in the Midwest compared to sites where the species is considered rare in the east. Chapter II outlines greenhouse and field removal experiments in which the types of host plants growing with *P. lanceolata* were manipulated. In the greenhouse, *P. lanceolata* growth, survival, and

flowering were lower when it was growing with invasive compared to native graminoids. However, differences in *P. lanceolata* growth and survival when natives versus non-native were removed in the field varied from year to year due to succession of native shrubs at the site during the study. Chapter III asks how the population growth of *P. lanceolata* differs in uninvaded and invaded patches using an Integral Projection Model to perform population projections, sensitivity and elasticity analyses, and a life table response experiment. The population growth rate of *P. lanceolata* in uninvaded patches was lower than in invaded patches due to the succession of native shrubs in uninvaded patches. Chapter IV describes a metapopulation model for the invaded population of *P. lanceolata* in Massachusetts. The quasi-extinction probability was significantly affected by probabilities of dispersal, positive correlations in vital rates between sites, and catastrophes. These data will be used to update the management plan for *P. lanceolata*.

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INTRODUCTION

The preservation of rare species is one of the most pressing issues faced by conservation biologists (Primack 2004). An assessment of 20,892 species in 2000 showed that one-third of the native flora and fauna in the United States are of conservation concern. The same study revealed that flowering plants in the United States have the largest number of species at stake of extinction (Master *et al.* 2000). Conservative estimates of the rate of extinction are 100 to 1000 times greater than background levels (Lawton and May 1995). Given currently rapid rates of extinction and large numbers of species at risk of imperilment conservationists must identify the primary threats to rare species in order to create effective management and recovery plans. A review of approximately 2,500 imperiled or federally listed species in the United States found that the highest-ranking threat was habitat destruction and degradation, affecting 85% of species analyzed. Competition with or predation by non-native invasive (hereafter referred to as invasive) species was the second greatest threat to imperiled species, affecting 49% of the analyzed species (Wilcove *et al.* 2000).

Numerous studies illustrate how introduced species may alter natural areas in which rare species occur. The introduction of top predators to food webs may have devastating direct effects on prey. For instance, the introduction of feral cats (*Felis catus*) to Stewart Island in New Zealand caused a dramatic decline in the number of Kakapo (*Strigops habroptilus*), a rare flightless parrot (Powlesland *et al.* 1995). Invasive plants may alter ecosystem-level properties of natural areas, such as nutrient cycles and disturbance regimes. Changes in the nutrient cycling of wet lowland forest in Hawaii by a nitrogen-fixing tree, Peacocks Plum (*Falcateria moluccanna*), facilitated increases in

other non-native species and caused decline of dominant native species (Hughes and Denslow 2005). In western North America, the alien annual Cheatgrass (*Bromus tectorum* L.) has changed the fire regime by increasing the frequency of hot fires, which has negatively affected fire-sensitive native plants (Brooks *et al.* 2004). In ecosystems altered by invasive species, rare species may be especially endangered due to their inherently small numbers, low competitive abilities, and restricted geographic ranges (Walck *et al.* 1998). Per se, it is a common belief that invasive species threaten native, rare species (Campbell 1996).

Although invasive species are regarded as a primary threat to endangered species, direct impacts of invasive species on rare populations remain largely anecdotal (Farnsworth 2004). Most often threats to rare species are identified based on expert opinion or observations that are not supported by experimental evidence or quantitative data (Wilcove *et al.* 2000). Of the handful of published papers that experimentally test the effects of invasive plants on rare plant species, some studies support the common belief that invasives negatively affect rare species (Walck *et al.* 1998, Harrod and Halpern 2005) whereas others exhibit contrary evidence (Munk *et al.* 2002, Miller and Duncan 2004).

Greenhouse studies suggest that invasive plants are detrimental to imperiled plant species. In a de Wit replacement series experiment Short's Goldenrod (*Solidago shortii* Torr. & Gray), a rare aster in northeastern Kentucky, was an inferior competitor to the invasive Tall Fescue (*Festuca arundinacea* Schreb.). When grown in pots with *F. arundinacea*, *S. shortii* exhibited decreased height and flowering (Walck *et al.* 1998). In greenhouse experiments the invasive biennial Teasel (*Dipsacus sylvestris* Huds.)

adversely affected a rare endemic of New Mexico, Sacramento Mountains Thistle (*Cirsium vinaceum* Woot. & Standl.). *Cirsium vinaceum* growth was significantly decreased when grown with *D. sylvestris*, but the growth of *D. sylvestris* was unaffected by the presence of *C. vinaceum* (Huenneke and Thomson 1995).

Some field experiments support the common belief that invasive species threaten rare plants. In the forests of eastern Washington, the rare endemic herb Thompson's Clover (*Trifolium thompsonii* Morton) responded positively to removal of competing ground layer vegetation composed primarily of the invasive Cheatgrass (*Bromus tectorum*). Survival of adult plants was greater in removal treatments (89%) than in no-removal control treatments (69%). After three years of release from competition with other ground layer vegetation, *T. thompsonii* individuals produced 160-389% more flowering stems and flowering heads and ~63% more leaves than untreated plants (Harrod and Halpern 2005). In California grasslands, introduced grasses had a significantly negative effect on the survivorship to reproduction, plant size, and nutlet production of a re-introduced population of large-flowered Fiddleneck (*Amsinkia grandiflora*) (Pavlik *et al.* 1993). *Solidago shortii* in early successional habitats of northeastern Kentucky responded positively to removal of the invasives Crown Vetch (*Coronilla varia* L.) and Tall Fescue (*F. arundinacea*). Seedlings of *S. shortii* emerged only in plots where invasives were clipped and removed. Within the first year of treatments, *S. shortii* plants in the removal plots exhibited a three-fold increase in flowering over individuals in non-clipped control plots (Walck *et al.* 1998).

Other field experiments suggest that invasives may only have a negative influence on rare plant species only at particular stages in their life cycle or in specific habitat types. In California grasslands the removal of invasive grasses, such as Ripgut Brome (*Bromus diandrus* Roth), resulted in higher rates of seedling recruitment for the endangered endemic Dune Primrose (*Oenothera deltoides* ssp. *howellii* (Munz) W. Klein). However, removal treatments had no effect on the survival of adult *O. deltoides.* In the same study, differences in habitat types also influenced the effects of the invasives removal treatments. Sites that naturally supported recruitment of *O. deltoides* showed a smaller removal treatment effect via higher total recruitment, but decreased adult survivorship, than sites experiencing restoration through planting (Thomson 2005). A study in New Zealand on the effects of invasive Hawkweeds (*Hieracium* sp.) on the rare cress *Pachycladon cheesemanii* also showed differing results for removal treatments in different habitats. Removal of *Hieracium* sp. increased the germination and seedling growth rates of *P. cheesemanii* in forested and open rocky outcrop habitats, but not in open tussock grasslands (Miller and Duncan 2004).

On the other end of the spectrum, some field studies show no negative effect of invasives on rare plants. In the mesic floodplains of Wyoming, the rare Colorado Butterfly plant (*Gaura neomexicana* Woot.) showed no response in vegetative growth, seed capsule production, or rosette density as a result of removal of the invasive Canada Thistle (*Cirsium arvense* (L.) Scop.). *Gaura neomexicana* did, however, exhibit increased recruitment of rosettes in response to removal of all other neighboring forbs, grass, and litter. The results of this study suggest that disturbances such as grazing and fire that decrease the dense vegetative cover and litter surrounding *G. neomexicana* may be more

effective in its recovery than the removal of invasive species alone (Munk *et al.* 2002). Similarly, weeding of the invasive grasses Jungle Rice (*Echinochloa colona* (L.) Link) and Hooked Bristlegrass (*Setaria verticillata* (L.) Beauv.) in the dry lowlands of Hawaii proved to be unnecessary for the persistence of the endemic fern Hawaiian Pepperwort (*Marsilea villosa* Kaulfuss) (Wester 1994).

The handful of published empirical studies available for making conservation decisions regarding the threat of invasive species to rare plants paint a less than clear picture. The scant quantitative data range from supporting to refuting the widespread belief that invasives are detrimental to rare plants. Furthermore, most studies focus on the competitive interactions between invasive and rare species. The emphasis on competition experiments may divert attention away from other important interactions between invasive and rare plants. For instance, Thomson (2005) found that for *O. deltoides* the strongest impact of invasives was on the inhibition of germination due to decreased soil disturbance.

Rare species with unique community-level interactions, such as the hemiparasites, may benefit more from knowledge regarding host-plant rather than competitive interactions with invasives (Marvier and Smith 1997). While there have been a number of studies investigating interactions between native host plants and native hemiparasites (*e.g*, Adler 2002; Gibson and Watkinson 1991; Lawrence and Kaye 2008), interactions between non-native invasive host species and native hemiparasites remain relatively understudied. Further, the few studies addressing the effects of non-native invasive hosts on native hemiparasites have yielded conflicting results. For example, in an outdoor pot experiment, the rare hemiparasite *Cordylanthus maritimus* ssp. *maritimus* Nutt. ex Benth.

produced fewer flowers when grown solely with the non-native invasive annual grass, *Parapholis incurva* (L.) C.E. Hubbard, than when it was grown with the native perennial grass, *Distichlis spicata* (L.) Greene, even though the number of haustorial connections between hemiparasite and host were the same for both *P. incurva* and *D. spicata* (Fellows and Zedler 2005). This result suggests that growth with unsuitable non-native invasive hosts has high resource allocation costs for *C. maritimus* ssp. *maritimus* in addition to decreasing its reproductive capacity. In contrast, in a field experiment in the woodlands of South Australia, the native stem parasite *Cassytha pubescens* R. Br. had higher photosynthetic and growth rates when growing on a non-native invasive host, *Cytisus scoparius* (L.) Link, than when attached to a native host, *Leptospermum myrsinoides* Schltdl. (Prider *et al.* 2009). That non-native invasive species may either reduce (*Cordylanthus maritmus* ssp. *maritimus*) or enhance (*Cassytha pubescens*) growth and/or fecundity illustrates that further investigations of the relationships between hemiparasites and their hosts, native or non-native, are needed.

Pedicularis lanceolata Michx. is a regionally rare hemiparasitic plant that is state listed as Endangered in Massachusetts (Brumback 1997). A recent management plan that I co-authored for *P. lanceolata* in Massachusetts identified invasive species as a primary threat to the rare hemiparasite (Farnsworth *et al.* 2007). In addition the conservation and research plan published by the New England Wild Flower Society that was written for *P. lanceolata* also identified invasives as a threat to the species (Allard 2001). However, there is no quantitative evidence that invasives threaten *P. lanceoalata*. The research this dissertation addresses aims to provide such quantitative information on the interactions between *P. lanceolata*, native, and invasive species. A brief description of the natural

history of *P. lanceolata* precedes the dissertation chapters. Chapter I outlines a study that documented associated species and identified potential hosts of *P. lanceolata* throughout its geographic range. The second chapter describes greenhouse and field removal experiments where the numbers of native and invasive host plants were manipulated. Chapter III compares the demography of *P. lanceolata* growing in uninvaded and invaded patches with sensitivity and elasticity analyses, a life table response experiment, and projections of population growth rates from deterministic and stochastic models. Finally, chapter IV describes the metapopulation dynamics of the invaded population of *P. lanceolata* in Massachusetts.

Natural History of *Pedicularis lanceolata*

Swamp Lousewort (*Pedicularis lanceolata*; family Orobanchaceae) is an erect perennial herb of periodically inundated open areas. *Pedicularis lanceolata* has solitary or branched stems that are smooth to sparsely hairy and commonly grow 20 to 80 cm (8-32 in.) in height (but can be up to 115 cm; 45 inches) (Gleason and Cronquist 1991). The leaves are opposite, stalkless to short-stalked, and typically 5-10 cm (2-4 in.) long. The pinnate (feather-like) lobes of the leaves reach less than halfway to the mid-vein. The showy cream-colored to yellow flowers are 1.5-2 cm (0.6-0.8 in.) long. The stalkless flowers occur in spikes (unbranched elongated inflorescences) on the end of the stem and in the upper leaf axils. The petals fuse to form a two-lipped flower. The upper petals form a hood-like upper lip (galea) that is untoothed. Bumble bees (*Bombus* spp.) are the primary pollinators for this obligate out-crossing plant (Macior 1969). The fruit is a brownish egg-shaped capsule that contains many tiny, brown winged seeds. In Massachusetts, the primary setting for this dissertation research, *P. lanceolata* emerges in late April, flowers from August to September, and sets seed in mid- to late October.

Pedicularis lanceolata is a generalist hemiparasitic plant (Piehl 1965). Hemiparasites are capable of producing sugars through photosynthesis, but still require water and nutrients from host plants obtained, through root connections called haustoria, to complete their life cycles (Heide-Jørgensen 2008). On average, haustoria of *P. lanceolata* are 1.5 mm in their longest dimension (Piehl 1965). In an experiment conducted in a growth chamber, *P. lanceolata* seedlings grown in sterile soil without a host plant did not live longer than 81 days (Lackney 1981). When grown in the laboratory at a pH of 6.2 on petri dishes supplemented with a mineral nutrient medium, *P.*

lanceolata seedlings developed similarly to seedlings planted in soil with a known host (Lackney 1981). In the same experiment, the growth of *P. lanceolata* seedlings was stunted when they were sown on petri dishes at a pH of 7.1 or when supplemented with sucrose, fructose, glucose, casein hydrolysate, glutamine, kinetin, giberellic acid, or indoleacetic acid. These results of Lackney (1981) suggest that *P. lanceolata* relies on host plants for water and minerals rather than organic compounds.

Swamp Lousewort grows in open areas that are periodically flooded such as wet meadows, marsh edges, and stream banks (Allard 2001). The documented range of Swamp Lousewort spans Massachusetts to Georgia on the east coast of the United States and west to Missouri and Manitoba, Canada (NatureServe 2009). Some habitats that *P. lanceolata* occupies are found throughout the species geographic range, such as stream sides and power line right-of-ways. However, other habitats that *P. lanceolata* occupies are only found in a particular portion of its range (*e.g.*, wet prairies in the Midwest, tidal wetlands along the eastern coast).

Pedicularis lanceolata is rare along the eastern coast of the United States, but relatively common in the Midwest (NatureServe 2009). It is historically known from Delaware and Kentucky. In New England, *P. lanceolata* has been documented in Connecticut and Massachusetts (Allard 2001). Connecticut currently lists *P. lanceolata* as a Species of Concern, while Massachusetts lists the species as Endangered (Brumback 1996). In Massachusetts, *P. lanceolata* is currently known only from Hampden and Hampshire Counties (Fig. 0.1a). Historical Massachusetts records document its previous existence in Franklin, Suffolk, and Worcester Counties (Fig. 0.1b).

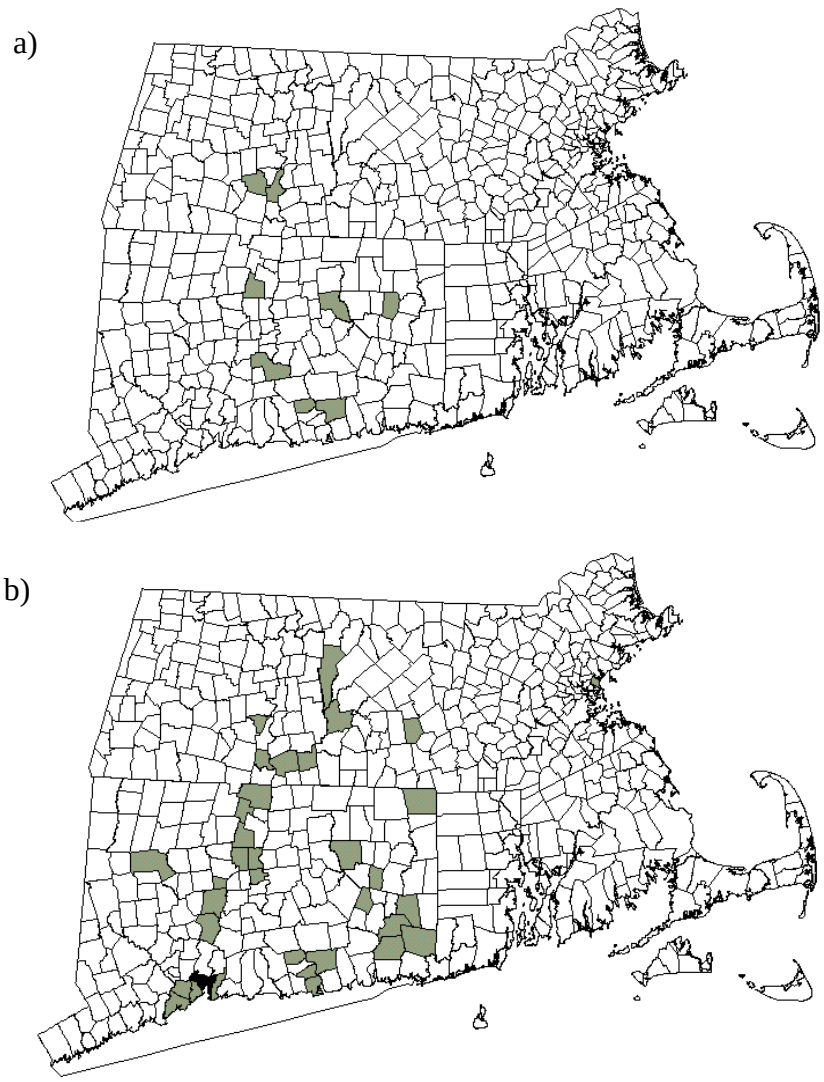

Figure I.1. Both a) current and b) historic distributions of *P. lanceolata* in New England. Towns shaded in grey had one to five occurrences, while those shaded in black had greater than five occurrences.

CHAPTER I

PLANT SPECIES ASSOCIATED WITH A REGIONALLY RARE HEMIPARASITIC PLANT, *PEDICULARIS LANCEOLATA* (OROBANCHACEAE), THROUGHOUT ITS GEOGRAPHIC RANGE

Abstract

Typically, non-native invasive plant species are considered a threat to rare native plants, but this generalization may not hold true for rare parasitic plants that depend upon host plants to complete their life cycles. It is essential to know what plant species a particular hemiparasitic species associates with in the field in order to determine host plant preferences and to make broader inferences about host plants. *Pedicularis lanceolata* is a hemiparasite that is regionally rare in New England and the southeastern margins of its range, but more abundant in the core of its range in the Midwest. I sought to compare the species associated with *P. lanceolata* in the core and margins of its range to determine if marginal populations have different associates from core populations. I hypothesized that *P. lanceolata* may be rare in the eastern United States because it encounters fewer suitable associates, and potentially more competitive invasive species, at the margins of its range than at the center of its range. In each of 22 populations of *P. lanceolata* I recorded abundances of all vascular plants growing near five focal *P. lanceolata* individuals. Different suites of species co-occurred with *P. lanceolata* in different parts of its range, but there were no significant differences across its range in the percent covers of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes. These results suggest that non-native invasive species do not pose greater threats to edge populations of *P. lanceolata* than to core populations.

The data suggest that candidates for potential hosts include members of the Asteraceae and Poaceae, as well as *Cirsium discolor, Clematis virginiana, Cornus amomum, Eupatorium maculatum, Eupatorium perfoliatum, Impatiens capensis, Lycopus uniflorus,* and *Vernonia gigantea* These data provide baseline data for future manipulative studies on host-preference of *P. lanceolata*.

Introduction

Approximately 4,500 of the world's plants are holoparasites (plants lacking chlorophyll and completely dependent on host plants to survive) or hemiparasites (plants with chlorophyll that rely on host plants for supplemental resources to complete their life cycle) (Heide-Jørgensen 2008). The availability of suitable hosts is critical to rare hemiparasites, whether they are specialists utilizing a single host species or generalists capable of parasitizing a suite of hosts (Marvier and Smith 1997).

Rare native hemiparasites co-occurring with non-native, invasive species pose a management conundrum. A review of approximately 2,500 imperiled or federally listed plant and animal species in the United States concluded that competition with or predation by invasive species is the second greatest threat to imperiled species, affecting 49% of the analyzed species (Wilcove et al. 1998). As such, the management of rare plants usually involves removing or controlling the density of non-native invasive species co-occurring with them. Such management, however, may not be appropriate for rare hemiparasitic plants that have unique interactions with host plants. If invasive plants co-occur with rare, generalist hemiparasites and serve as alternate hosts for the hemiparasites, or if facilitative (parasitic) interactions between hosts and hemiparasites outweigh negative competitive interactions, it may be detrimental to remove or control

the co-occurring invasive plants. Whereas a number of studies have investigated interactions between native host plants and native hemiparasites (e.g., Adler 2002; Gibson and Watkinson 1989; Lawrence and Kaye 2008), interactions between non-native invasive host species and native hemiparasites remain relatively understudied. Further, the few studies addressing the effects of non-native invasive hosts on native hemiparasites have yielded conflicting results (Fellows and Zedler 2005; Prider et al. 2009).

Regionally rare species (i.e., Division 2 rare taxa according to Brumback et al. (1996)) that reach the edge of their geographic range in the Northeast and that have less than 20 occurrences in New England are ideal for studies on the effects of native and non-native invasive plants on native hemiparasites, allowing for comparisons between areas where such species are common within their ranges and areas in which they are rare. Regionally rare species also enable investigation into correlates of rarity because conditions in which a species is common can provide hints as to limiting factors at the edge of the range where the species may be rare (Kunin and Gaston 1997; Rabinowitz 1981). Finally, comparisons between different areas of regionally rare species' geographic ranges can help to adapt management approaches to the particular needs of common and rare populations. Such adaptive management is important because at the edge of a species' range there is greater potential for evolutionary change (Grant and Antonovics 1978; Lesica and Allendorf 1995). For instance, populations at the periphery of a species' range may exhibit founder effects due to isolation from gene flow compared to more centrally located populations (Lammi 1999).

Pedicularis lanceolata Michx. is a "regionally rare" North American generalist hemiparasite; that is, it is listed as rare in the states at the Northeastern and Southeastern portions of its range, but is considered secure and has more numerous populations in the geographic heart of its range in the Midwest (NatureServe 2009). Prior studies have provided some data on interactions between *P. lanceolata* and some of its host species. Foster (2003) studied the effects of *P. lanceolata* on three native (*Chelone glabra* L.*, Juncus effusus* L.*,* and *Scirpus cyperinus* (L.) Kunth) and one non-native invasive (*Phalaris arundinacea* L.) hosts in a container experiment to see if *P. lanceolata* could be used as a biological control agent on *P. arundinacea*. Seedlings of *P. lanceolata* established haustoria with all four hosts in this study. The biomass of *P. arundinacea* was decreased only when *P. lanceolata* was accompanied by the other native species, suggesting that competition by multiple native species was needed to depress growth of *P. arundinacea* (Foster 2003).

Previous studies also have provided information on potential or known hosts of *P. lanceolata* (i.e., species with which *P. lanceolata* are known to form haustoria). Macior (1969) and Farnsworth et al. (2007) recorded a total of 73 associated species of *P. lanceolata* in the field in Ohio and Massachusetts, respectively, but could not confirm if *P. lanceolata* formed haustorial connections to these species (Table 1.1). Other studies documented direct haustorial connections between *P. lanceolata* and 29 host species through root excavations in the field (Piehl 1965), lab experiments (Lackney 1981), and outdoor container experiments (Foster 2003) (Table 1.1). Only two of the 29 species with which *P. lanceolata* was known to form haustoria were invasive species: *Frangula alnus*

Mill. and *Phalaris arundinacea* L. (Table 1.1). Three quarters of these known hosts came from a study of a single site in Michigan, the geographic center of *P. lanceolata*'s range (Piehl 1965).

The first objective of this study was to document plant species growing with *P. lanceolata* in populations in the center of its range in the Midwest where the species is common (henceforth, the "core") and at the margins of its range in the Northeast and Southeast where the species is rare (henceforth, the "edge"). While some habitats, such as stream banks, are common to different regions where *P. lanceolata* occurs, other habitats are unique to certain portions of its range, such as prairies in the Midwest or tidal wetlands along the east coast. As such, I hypothesized that marginal populations of *P. lanceolata* in the Northeastern and Southeastern states would establish associations with different species from those associated with populations of *P. lanceolata* in the Midwest.

The second objective of this study was to determine whether the types and relative abundances of native and invasive species associated with *P. lanceolata* differed between core and edge geographic areas. I hypothesized that *P. lanceolata* in the edge of its range where it is considered as rare occurs more frequently with invasive species that are potentially less preferred hosts or stronger competitors for resources. If populations along the eastern coast of the United States where *P. lanceolata* is considered rare occur more frequently with less suitable associates (i.e., invasive species) than populations in the Midwest where the species is considered common, then I predict that the proportions of invasive species associated with *P. lanceolata* will be higher in eastern populations. Alternatively, if populations of *P. lanceolata* throughout its geographic range are similarly associated with invasive species, then I predict that the relative abundances of

native and invasive species will not differ between Midwestern and eastern populations. To identify finer-scale differences in associated species due to latitudinal variation, I compared edge populations at the regional level (i.e., Northeast, Southeast). I was not able to confirm the hosts utilized by *P. lanceolata* or whether or not interactions with associated species were competitive or beneficial, but the data presented here do help to identify a suite of potential host plant species.

Methods

Study species

Laboratory studies show that *P. lanceolata* is an obligate hemiparasite: seedlings become chlorotic and die when grown without a host (Lackney 1981). In observational field studies and laboratory and outdoor container experiments, *P. lanceolata* acts as a generalist, forming haustorial connections with a number of species to obtain water and mineral nutrients (Foster 2003; Lackney 1981; Piehl 1965) (Table 1.1).

Pedicularis lanceolata grows in habitats that are periodically inundated, such as wet meadows, prairies, swamps, freshwater tidal marshes, and stream sides, and other, early-successional habitats (Allard 2001). The global conservation status of *P. lanceolata* is secure (G5), but it is listed as historic, endangered, threatened, or a species of concern in 15 of the 25 states in which it occurs in the United States (NatureServe 2009) (Figure 1.1). Most of the states in which *P. lanceolata* is considered rare are along the eastern coast of the United States, with the exception of Kentucky, where the species is possibly extinct and is known only from historic records (NatureServe 2009). *Pedicularis lanceolata* is most secure (S4) along the northern edge of its range in Manitoba and Ontario (NatureServe 2009).

Field methods

I sampled 11 populations of *P. lanceolata* in Illinois and Wisconsin where the species was classified by the state as common, and 11 populations in Connecticut, New York, North Carolina, and Tennessee where the species was state-listed as rare in July and August of 2007 (Figure 1). In the states where *P. lanceolata* was considered rare, there were 2-17 extant populations per state of the species that varied in size from three to hundreds of individuals. Populations were defined as groups of co-occurring organisms of the same species that were likely to interbreed. Macior (1969) showed that *P. lanceolata* is an obligate outcrossing species pollinated by bumblebees (*Bombus* spp.), particularly *Bombus vagans* Smith. While the foraging distances of *B. vagans* have not been investigated in detail, there were data on foraging ranges for other species in the genus. Knight et al. (2005) conservatively estimated the maximal foraging range for the genus as 758m in the United Kingdom based on studies that used molecular markers. Thus, each site in this study was considered a separate population because all sites were further than ten kilometers away from one another.

I selected sampling sites based upon the most recently updated state Natural Heritage and Endangered Species Program field forms for states where *P. lanceolata* was classified as rare, and herbarium specimens dating back to 1990 for locations where the species is considered common. I did not seek to sample similar types of habitats in each of the three sectors because one objective of this study was to see if *P. lanceolata* occurred with different species at core and edge sites. For this same reason, I sampled along a broader latitudinal gradient in the edge than in the core in order to capture any differences in associated species and potential hosts due to climatic and other differences

between the southeast and northeast margins of the range. Despite the greater aggregation of sites in the Midwest, the habitats sampled were variable (e.g., fens, stream sides, prairies, lake shores, city parks), so the closer proximities of sites in the Midwest should not have biased the results in regards to habitat types. Logistical constraints and differences in the numbers of extant populations in different states resulted in an unbalanced design, with seven populations in the Midwest, four in the Southeast, and seven in the Northeast.

At each site, I set up a transect through the center of the population and used random numbers to select plants based on their positions relative to the transect (Haahr 2006). Abundances in six cover classes (<1%, 2-5%, 6-25%, 26-50%, 51-75%, and 76-100%) of all vascular plant species were recorded within half-meter-radius circular plots centered on five focal *P. lanceolata* plants per population. The scarcity of *P. lanceolata* in many of the edge, and some of the core, populations limited the number of focal plants sampled in each population to five. I chose the size of the plots based upon my previous root excavations of five plants in the Midwestern United States, that revealed that the roots of *P. lanceolata* extended approximately one-half meter from the base of an individual. Thus, I assumed that associated vascular species occurring within one-half meter of the focal *P. lanceolata* plant were available as potential hosts. Also, associated plants within one-half meter of *P. lanceolata* were the most likely to compete with it for light. I did not collect data on the species pool at the sites beyond the sampling that I did around the focal *P. lanceolata* individuals. Other papers on hemiparasitic species have done this, and analyzed the data with an association analysis to see if the hemiparasite was correlated with certain associated species. However, Gibson and Watkinson (1989)

showed that an association analysis of *Rhinanthus minor* only revealed two potential hosts, whereas direct examination of the plants' roots showed that the plants were forming haustorial connections with 20 species. Further, there was not great variation at any of the 22 sites in species present in areas with or without *P. lanceolata*. As such, I chose to sample more populations, only recording information from plots with *P. lanceolata* present, rather than visiting fewer populations while sampling plots with and without *P. lanceolata.* All vascular plants were identified to species using Gleason and Cronquist (1991), with the exception of some *Carex* species for which positive identification was not possible because perigynia were undeveloped at the time of sampling. Unidentifiable *Carex* species were treated as different un-named taxa based on vegetative morphology. Nomenclature followed the Integrated Taxonomic Information System (2010). Voucher specimens are housed in the herbaria of the Universities of Massachusetts, Tennessee, and Wisconsin.

Data analysis

To visualize differences in the species associated with *P. lanceolata* throughout its range, I analyzed the abundance data of all species encountered with non-metric multidimensional scaling (NMDS) using Bray's distance measure and two dimensions to plot an ordination showing relationships between species and sites (McGarigal et al. 2000). Non-metric multidimensional scaling was employed rather than correspondence analysis (CA) or detrended correspondence analysis (DCA) because as a nonparametric procedure NMDS was less sensitive to outliers and made no assumption that the species' distributions along the underlying gradient exhibited unimodal or linear responses (McGarigal et al. 2000). To determine whether population-level differences in associated

species were due to the greater latitudinal gradient sampled in the edge, I overlaid ellipses onto the ordination plot showing the standard deviations of the point scores for species within each portion of the range (core or edge) and region (Midwest, Northeast, or Southeast) using the 'ordi.ellipse' function from the vegan package in the R statistical software (R Development Core Team, Vienna, Austria).

All co-occurring plant species were categorized into the following groups: natives, non-native invasives, non-native non-invasives, and non-invasive species having co-occurring native and non-native genotypes (Table 1.1). Classifications of species by origin and invasiveness in the United States Department of Agriculture (USDA) PLANTS database were inconsistent with individual state classifications, so associated non-native species were only considered invasive when they were listed as invasive by the USDA and at least one other state (USDA 2009). References for individual states were: Connecticut (Mehroff et al. 2003), Illinois (Howe et al. 2008), North Carolina (Smith 2008), New York (Invasive Plant Council of NY State 2005; O'Neill, 2008), Tennessee (Franklin et al. 2004; Miller 2003), and Wisconsin (Reinartz 2003; Howe et al. 2008). Species with both non-native and native genotypes included *Achillea millefolium* L., *Poa pratensis*, *Ranunculus acris* L., *Rubus idaeus* L., *Taraxacum officinale* F.H. Wigg, and *P. arundinacea* (USDA 2009). *Phalaris arundinacea* L. (Gifford et al. 2002) was one of the most abundant co-occurring species at many of the study sites, suggesting that the non-native genotype may have been at the sites studied. Thus, I performed two separate analyses where *P. arundinacea* was treated either as non-native invasive or a

species with native and invasive genotypes. I confirmed that none of the unknown *Carex* species were considered non-native invasive based on comparisons of vegetative characters with known invasive *Carex* species.

To determine whether there were regional or sub-regional differences in the percent covers of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes associated with *P. lanceolata*, I performed four nested analyses of variance (ANOVAs). I averaged the relative abundances of all species in a category (e.g., natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes) over the five independently sampled plants in each population to emphasize population-level rather than plot-level differences. Since relative abundances were in percent cover classes, the averages were based on the median value for the range of values in a cover class (e.g., for the cover class ranging from 1% to 5% I used 3% to calculate the average). The response variables in the four ANOVAs were these population-level averages for the percent covers of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes. Plot-level averages were arcsine square-root transformed to meet the model assumptions of residual normality and homogeneity of variance. I tested the response of either average cover of natives, non-native invasives, non-native non-invasives, or species with native and non-native genotypes to two predictor variables: part of range (i.e., core, edge), and region nested within part of range (i.e., Northeast and Southeast nested within edge; Midwest nested within core). Region was included to test for any effects due to latitudinal

differences in the species pools of associated species in the populations sampled. All statistical analyses were performed using the R statistical software version 2.10.1 (R Development Core Team Vienna, Austria).

Results

Pedicularis lanceolata co-occurred with a total of 264 different species representing 634 families across the 22 sites sampled (Table 1.1). The families with the most representatives were the Asteraceae and the Poaceae. *Lycopus uniflorus* Michx. occurred most frequently in all three regions. Of the 264 species documented, 156 species were found in the Midwest (including 74 species only found in this region), 154 in the Northeast (63 unique to this region), and 82 in the Southeast (31 unique to this region) (Table 1.1). None of the species occurred at all 22 sites. Nine percent of the plots sampled at the 22 sites did not contain any of the hosts known to form haustoria with *P. lanceolata* (Foster 2003; Lackney 1981; Piehl 1965). The ordination showed that the standard deviations of the species' ordination scores for the core and edge overall did not overlap, although the standard deviations of the Midwest and Northeast regions' species' ordination scores overlapped. The Midwest and Northeast regions shared more co-occurring species than either did with the Southeast region (Figure 1.2).

The average proportion of native species was much greater than the average proportion of non-native invasive or non-native non-invasive species in each part of the range (core or edge) and region (Table 1.2; Figure 1.3). Sixteen non-native invasive and 23 non-native non-invasive species co-occurred with *P. lanceolata* in the 22 populations sampled. Two of the 16 non-native invasive species were found in both edge and core populations (*Rhamnus frangula* L. and *Lonicera morrowii* A. Gray). *Phalaris*

arundinacea and *R. frangula* were the predominant non-native species associated with *P. lanceolata* in the Midwest. In the Northeast, the most common non-native invasive species or species with co-occurring non-native and native genotypes growing with *P. lanceolata* were *Cynanchum louiseae* Kartesz & Gandhi, *Lythrum salicaria* L., and *P. arundinacea*. In the Southeast, *Lonicera japonica* Thunb. and *Ligustrum vulgare* L. were the non-native invasives that occurred with *P. lanceolata* at the highest frequencies. The percent covers of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes did not differ between core and edge populations or regions of edge populations (Table 1.2). The ANOVA results were consistent regardless of whether *P. arundinacea* was classified as a non-native invasive species or as a species with native and non-native genotypes. As such, I present only the results of the analysis where *P. arundinacea* was treated as a non-native invasive species (Table 1.2).

Discussion

This study has documented associated species for a regionally rare hemiparasite, *P. lanceolata*, across a broad geographic extent, and found that there were no significant differences among edge and core populations in the relative abundances of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes. For *P. lanceolata*, greenhouse (Foster 2003; Lackney 1981) and root excavation (Piehl 1965) studies have provided data on hosts with which haustoria were formed, but the majority of the documented species came from a single study in Michigan (Piehl 1965). Hosts with which *P. lanceolata* formed haustoria documented from these past studies did not occur in 9% of the plots I sampled, suggesting that there were undocumented hosts of *P. lanceolata*.

The ordination analysis showed that associated species in the Midwest and Northeast had more overlap with one another than with the Southeast (Figure 1.2). The Northeast and Midwest regions lie on similar latitudes, so this result was likely due to latitudinal differences in species distributions. In the ordination, there were a number of distinct species that projected far from regional centroids and did not fall within the standard deviations of species' scores for other regions, suggesting that some species were exclusive to a particular region. Data in Table 1.1 also showed that there were a number of species that were unique to each region. These results suggested that *P. lanceolata* grew with some unique species in different parts of its range.

Based on the data, *L. uniflorus* was a candidate for a host plant because it occurred most frequently and occasionally at high abundances in all three sub-regions. In the Midwest, *P. lanceolata* was most often found growing with *Cirsium discolor* (Muhl. ex Willd.) Spreng., *Eupatorium maculatum* L., and *Equisetum palustre* L. Likely candidates for potential hosts in the Northeast included *Cornus amomum* P. Mill. and *Eupatorium perfoliatum* L. In the Southeast, *Clematis virginiana* L., *Impatiens capensis* Meerb., and *Vernonia gigantea* ssp. *gigantea* (Walt.) Trel. commonly co-occurred with *P. lanceolata*. Also, the families of plants most frequently associated with *P. lanceolata* were the Asteraceae and Poaceae, so members of these families were also candidates for potential hosts.

Of the populations sampled, the percent cover of non-native invasives, non-native non-invasives, and species with native and non-native genotypes was much smaller than that of native species (Figure 1.3). This high ratio of native to non-native species could be due to a number of reasons. The sites sampled in this study could have been at early

stages in the invasion process. Alternatively, *P. lanceolata* may not have been able to establish haustoria with many invasives and thus did not occur with them. *Pedicularis lanceolata* also could have been associated with some other variable (e.g., historical land-use practices) that resulted in sites being less invaded. The differences between non-native invasive species' cover among all populations all were less than five percent and there were no significant differences between the percent covers of natives and non-natives. These results implied that at the sites sampled, the edge populations were not more likely to be threatened by non-native species than the core populations. This conclusion should not, however, discount the relevance of future studies investigating the relationships between hemiparasites, native hosts, and non-native hosts because non-native invasives may be locally dominant at particular sites of interest. For instance, the only population of *P. lanceolata* in the entire state of Massachusetts has been heavily invaded by *P. arundinacea* (Farnsworth et al. 2007).

There were some limitations to this study that should be addressed. First, the number of plants sampled per population was low due to the scarcity of individuals in populations along the east coast where *P. lanceolata* was rare. One potential caveat to such a low sample size was that the associated species might not have been representative of a site. Small sample sizes were an inherent issue of working with rare species that were not locally abundant. Despite this limitation, it was reassuring that the associated species within different populations were not highly variable, so the sampling scheme presented here is likely a good representative of the associated species at the sites sampled. A second limitation of this study was that haustorial connections between *P. lanceolata* and its associated species were not confirmed, so the data provided suggested

potential rather than known hosts. While it was not possible to quantify haustorial connections in the field due to the rarity of *P. lanceolata* in many of the sites sampled, the documentation of associated species in this study was relevant for comparing characteristics of populations that occur where the species was rare versus where the species was common.

The results of this study are valuable for tailoring the management of core and edge populations of *P. lanceolata* and for providing data on host plants that can be used to broaden inferences from subsequent field or greenhouse experiments. Given their potential management implications, future studies on the effects of non-native invasive species on hemiparasites, such as *P. lanceolata*, should include a field component and management treatments, as well as a greenhouse treatment. Lawrence and Kaye (2008) showed that greenhouse experiments alone on the rare hemiparasite *Castilleja levisecta* Greenm. with different native hosts were poor predictors of how the hemiparasite and hosts interacted in the field because they lacked important indirect effects between host and hemiparasite exerted by vole herbivory. Without a field component, experiments on non-native invasive species and hemiparasites may not accurately portray host-hemiparasite interactions. Further, few experiments on hemiparasites include possible management scenarios (but see Petrů 2005). In combination with the extensive field survey data illustrated here, manipulative studies of *P. lanceolata* and other rare hemiparasites will provide many opportunities to better understand the interactions between hemiparasites and their native and non-native hosts (Chapter II).

Table 1.1. A list of all species growing with *P. lanceolata* in this study and previous studies. An asterisk (*) indicates species for which direct haustorial attachments between *P. lanceolata* and the species have been documented in the indicated studies . The numbers listed in for each region (Midwest, Northeast, or Southeast) are the proportion of sites where the species occurred within the region and the mean and variance of the percent cover of that species in the region. If a species was not found in a particular region in this study, but was previously documented in other studies, then the value for that species and region combination is 'N/A' for 'not applicable.'

Family and species	Previously documented associate	Midwest	Northeast	Southeast
Aceraceae				
Acer rubrum L.	Farnsworth et al. 2007	0.09, 0.02 ± 0.02	0.71, 2 ± 46	0.25, 6 ± 193
Alismataceae				
Sagittaria latifolia Willd.		0.18, 0.3 ± 4	0.14, 1 ± 41	0
Amaranthaceae				
Gomphrena globosa L.		0	0.14, 2 ± 47	0
Anacardiaceae				
Toxicodendron radicans (L.) Kuntze		0.09, 0.8 ± 12	0.29, 2 ± 47	0.25, 4 ± 137
Apiaceae				
Angelica atropurpurea L.		0.18, 2 ± 55	0	0
Cicuta bulbifera L.		0.27, 0.1 ± 0.09	0.14, 0.03 ± 0.03	0
Cicuta maculata L.	Farnsworth et al. 2007	0.09, 0.7 ± 26	0.29, 2 ± 80	0
* *Daucus carota* L.	Piehl 1965, Farnsworth et al. 2007	0.18, 0.06 ± 0.06	0.57, 3 ± 84	0.25, 0.05 ± 0.05
Hydrocotyle americana L.		0	0.14, 0.03 ± 0.03	0
Oxypolis rigidior (L.) Raf.		0.27, 3 ± 121	0	0.25, 0.8 ± 11
Sanicula marilandica L.		0.09, 1 ± 30	0	0
Apocynaceae				
* *Apocynum cannabinum* L.	Piehl 1965	N/A	N/A	N/A

Continued on next page

Table 1.1., continued

Araceae				
* *Peltandra virginica* (L.) Schott	Piehl 1965	N/A	N/A	N/A
Symplocarpus foetidus (L.) Salisb. ex Nutt.		0	0.14, 0.03 ± 0.03	0
Asclepiadaceae				
Asclepias incarnata L.	Farnsworth et al. 2007	0.27, 0.8 ± 26	0.29, 1 ± 41	0
Asclepias syriaca L.	Farnsworth et al. 2007	N/A	N/A	N/A
Cynanchum louiseae Kartesz & Gandhi	Farnsworth et al. 2007	0	0.29, 4 ± 123	0
Asteraceae				
Achillea millefolium L.		0.18, 0.05 ± 0.05	0.14, 1 ± 41	0.25, 6 ± 194
Ambrosia artemisiifolia L.	Farnsworth et al. 2007	0.09, 0.7 ± 26	0.14, 0.03 ± 0.03	0.25, 0.05 ± 0.05
Ambrosia trifida L.		0.09, 0.7 ± 26	0	0
Antennaria neglecta Greene		0.09, 0.3 ± 4	0	0
Arnoglossum plantagineum Raf.		0.09, 0.02 ± 0.02	0	0
Bidens cernua L.		0	0	0.25, 0.8 ± 11
Bidens connata Muhl. ex Willd.		0.09, 0.02 ± 0.02	0	0
Bidens frondosa L.	Farnsworth et al. 2007	0	0.14, 0.03 ± 0.03	0
Carduus arvensis (L.) Robson		0.09, 0.3 ± 4	0	0
Cirsium altissimum (L.) Hill	Macior 1969	N/A	N/A	N/A
Cirsium discolor (Muhl. ex Willd.) Spreng.		0.55, 4 ± 121	0.14, 1 ± 41	0
Doellingeria umbellate var. *umbellata* (P. Mill.) Nees		0	0.29, 2 ± 47	0
Eupatorium fistulosum Barratt		0	0	0.50, 2 ± 72
* *Eupatorium maculatum* L.	Piehl 1965, Farnsworth et al. 2007	0.63, 10 ± 228	1, 8 ± 185	0

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Table 1.1, continued

Eupatorium perfoliatum L.	Farnsworth et al. 2007	0.36, 4 ± 108	0.71, 4 ± 95	0.50, 3 ± 87
Euthamia graminifolia (L.) Nutt.	Farnsworth et al. 2007	0.36, 6 ± 208	0.43, 9 ± 261	0
Euthamia tenuifolia var. *tenuifolia* (Pursh) Nutt.		0.09, 0.9 ± 12	0	0
Helenium autumnale L.		0.18, 1 ± 30	0	0.25, 0.8 ± 11
Helianthus annuus L.		0.09, 2 ± 58	0	0
Helianthus decapetalus L.	Macior 1969	N/A	N/A	N/A
Helianthus giganteus L.		0.36, 5 ± 171	0	0
Hieracium caespitosum Dumort.		0.09, 1 ± 30	0.43, 3 ± 84	0
Lactuca sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Leucanthemum vulgare Lam.		0.09, 0.02 ± 0.02	0.43, 1 ± 41	0.25, 0.05 ± 0.05
Liatris scariosa var. *novae- angliae* Lunell		0	0.14, 0.4 ± 6	0
Machaeranthera parviflora Gray		0	0	0.25, 2 ± 72
Oligoneuron ohioensis (Frank ex Riddell) G.N. Jones		0.27, 5 ± 146	0	0
Oligoneuron riddellii (Frank ex Riddell) Rydb.		0.09, 0.7 ± 26	0	0
Packera schweinitziana (Nutt.) W.A. Weber & Löve		0.09, 0.04 ± 0.04	0	0
Rudbeckia fulgida var. *speciosa* (Wenderoth) Perdue		0	0	0.25, 0.8 ± 11
Rudbeckia laciniata L.		0	0	0.25, 0.8 ± 11
Solidago canadensis L.		0.36, 7 ± 202	0.14, 0.4 ± 6	0

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Table 1.1., continued

Solidago canadensis var. *scabra* Torr. & Gray	Macior 1969	0	0.14, 2 ± 80	0
Solidago gigantean Ait.	Farnsworth et al. 2007	0.55, 10 ± 213	0.43, 2 ± 80	0.50 , 3 ± 80
Solidago nemoralis Ait.		0.09, 0.04 ± 0.04	0	0
* *Solidago patula* Muhl. ex Willd.	Piehl 1965, Farnsworth et al. 2007	0	0.43, 7 ± 185	0.5, 2 ± 30
Solidago rugosa P. Mill.	Farnsworth et al. 2007	0	0.57, 7 ± 185	0
Solidago sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Solidago uliginosa Nutt.		0.18, 4 ± 106	0.43, 6 ± 195	0.25, 0.8 ± 11
Sonchus arvensis L.		0.27, 1 ± 33	0	0
Symphyotrichum boreale (Torr. & Gray) A. & D. Löve		0.09, 0.04 ± 0.04	0	0
Symphyotrichum laeve var. *laeve* (L.) A. & D. Löve		0.09, 1 ± 30	0	0
* *Symphyotrichum lateriflorum* var. *lateriflorum* (L.) A. & D. Löve	Piehl 1965	0	0.14, 2 ± 80	0.25, 2 ± 72
* *Symphyotrichum novae-angliae* (L.) Nesom	Piehl 1965, Macior 1969	0.45, 6 ± 185	0.57, 7 ± 184	0
Symphyotrichum pilosum var. *pilosum* (Willd.) Nesom	Macior 1969	N/A	N/A	N/A
Symphyotrichum praealtum var. *praealtum* (Poir.) Nesom		0.09, 0.3 ± 4	0	0
Symphyotrichum prenanthoides (Muhl. ex Willd.) Nesom		0.09, 1 ± 34	0	0

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Table 1.1, continued

Symphyotrichum puniceum var. *puniceum* (L.) A. & D. Löve	Farnsworth et al. 2007	0.36, 4 ± 127	0.29, 3 ± 84	0.50, 5 ± 145
Symphyotrichum sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Taraxacum officinale G.H. Weber ex Wiggers		0.45, 0.1 ± 0.1	0.57, 2 ± 46	0.50, 2 ± 72
Vernonia gigantea ssp. *gigantea* (Walt.) Trel.		0.09, 1 ± 30	0	0.75, 6 ± 196
Vernonia noveboracensis (L.) Michx.		0	0.14, 2 ± 47	0.25, 4 ± 93
Balsaminaceae				
* *Impatiens capensis* Meerb.	Piehl 1965, Farnsworth et al. 2007	0.55, 3 ± 78	0.43, 3 ± 84	0.75, 10 ± 235
Berberidaceae				
Berberis thunbergii var. *atropurpurea*		0	0.14, 1 ± 41	0
Betulaceae				
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Farnsworth et al. 2007	0	0.29, 8 ± 338	0.25, 3 ± 80
Bignoniaceae				
Campsis radicans (L.) Seem. ex Bureau		0	0	0.25, 0.8 ± 11
Boraginaceae				
Myosotis scorpioides L.	Farnsworth et al. 2007	0.09, 0.7 ± 26	0	0
Brassicaceae				
Alliaria petiolata (Bieb.) Cavara & Grande		0	0.14, 1 ± 41	0
Campanulaceae				
Campanula aparinoides Pursh.		0.55, 2 ± 75	0	0.25, 0.1 ± 0.1
Lobelia kalmia L.		0.18, 0.7 ± 26	0.14, 0.03 ± 0.03	0
Lobelia siphilitica L.		0	0.14, 0.03 ± 0.03	0
Caprifoliaceae				
Lonicera japonica Thunb.		0	0	0.25, 2 ± 30

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Table 1.1, continued

Lonicera morrowii Gray	Farnsworth et al. 2007	0.09, 1 ± 30	0.43, 2 ± 80	0.25, 0.05 ± 0.05
Lonicera tatarica L.		0.09, 0.5 ± 8	0	0
Viburnum acerifolium L.		0	0.14, 0.03 ± 0.03	0
Viburnum dentatum L.		0.09, 3 ± 124	0.14, 0.06 ± 0.06	0
Viburnum dentatum var. lucidum Ait.		0	0.43, 3 ± 116	0
Viburnum lentago L.		0.09, 0.7 ± 26	0.29, 1 ± 41	0
Viburnum nudum L.		0	0	0.25, 0.05 ± 0.05
Viburnum opulus var. *americanum* Ait.		0	0.14, 0.03 ± 0.03	0
Caryophyllaceae				
Cerastium fontanum ssp. *vulgare* (Hartman) Greuter & Burdet		0.09, 0.02 ± 0.02	0.14, 0.03 ± 0.03	0
Celastraceae				
Celastrus orbiculata Thunb.	Farnsworth et al. 2007	0	0.14, 2 ± 113	0
Celastrus scandens L.		0	0	0.25, 12 ± 494
Clusiaceae				
Hypericum mutilum L.		0	0	0.25, 0.8 ± 11
Hypericum perforatum L.		0.09, 0.04 ± 0.04	0.29, 1 ± 41	0.25, 0.05 ± 0.05
Convolvulaceae				
Calystegia sepium ssp. *sepium* (L.) R. Br.		0.09, 2 ± 58	0	0
Cornaceae				
Cornus amomum P. Mill.	Farnsworth et al. 2007	0.55, 5 ± 129	0.86, 5 ± 153	0
* *Cornus foemina* P. Mill.	Piehl 1965	0	0.29, 3 ± 116	0
Cornus rugosa Lam.		0	0.14, 0.4 ± 6	0
* *Cornus sericea* L.	Piehl 1965	0	0.14, 1 ± 41	0

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Table 1.1, continued

Cuscutaceae				
Cuscuta gronovii Willd. ex J.A. Schultes		0.09, 0.02 ± 0.02	0	0
Cyperaceae				
Carex communis Bailey		0.09, 1 ± 72	0	0
Carex conoidea Schkuhr ex Willd.		0.09, 3 ± 167	0	0
Carex crinita Lam.	Farnsworth et al. 2007	0	0	0.75, 5 ± 98
Carex hystericina Muhl. ex Willd.		0	0.14, 3 ± 151	0
Carex lacustris Willd.		0	0.14, 0.9 ± 12	0
Carex lasiocarpa Mackenzie ex Bright		0	0.14, 3 ± 116	0
Carex lupulina Muhl. ex Willd.		0	0.29, 2 ± 80	0
Carex lurida Wahlenb.	Farnsworth et al. 2007	0	0	0.25, 5 ± 285
Carex sartwellii Dewey		0.09, 0.7 ± 26	0	0
Carex sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Carex stricta Lam.		0.09, 4 ± 165	0.29, 2 ± 47	0
Carex vulpinoidea Michx.	Farnsworth et al. 2007	0	0.29, 4 ± 120	0
Cyperus sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Dulichium arundinaceum (L.) Britt.		0	0.29, 2 ± 80	0
Eleocharis acicularis (L.) Roemer & J.A. Schultes		0.09, 0.02 ± 0.02	0	0
Eleocharis rostellata (Torr.) Torr.		0.09, 0.7 ± 26	0.14, 1 ± 41	0
Rhynchospora capitellata (Michx.) Vahl	Farnsworth et al. 2007	N/A	N/A	N/A
Scirpus atrovirens Willd.		0.27, 3 ± 101	0.43, 4 ± 150	0

Continued on next page

Table 1.1, continued

* *Scirpus cyperinus* (L.) Kunth	Foster 2003, Farnsworth et al. 2007	N/A	N/A	N/A
Scirpus tabernaemontani (K.C. Gmel.) Palla		0	0.14, 1 ± 41	0
Droseraceae				
Drosera rotundifolia L.		0.09, 0.05 ± 0.05	0	0
Dryopteridaceae				
Onoclea sensibilis L.	Farnsworth et al. 2007	0.09, 1 ± 30	0.57, 6 ± 157	0
Equisetaceae				
* *Equisetum arvense* L.	Piehl 1965	0	0.43, 5 ± 152	0
Equisetum hyemale L.		0.09, 0.7 ± 26	0.14, 0.03 ± 0.03	0
Equisetum laevigatum A. Braun		0.27, 3 ± 101	0	0
Equisetum palustre L.		0.72, 12 ± 352	0.29, 6 ± 294	0
Equisetum variegatum Schleich. ex F. Weber & D.M.H. Mohr		0	0.29, 0.4 ± 6	0
Ericaceae				
Andromeda polifolia var. *glaucophylla* (Link) DC.		0	0	0.25, 4 ± 136
Fabaceae				
Amphicarpaea bracteata (L.) Fern.	Farnsworth et al. 2007	0.09, 0.02 ± 0.02	0.71, 0.5 ± 6	0.50, 9 ± 241
Apios americana Medik.	Farnsworth et al. 2007	0	0.14, 0.9 ± 12	0.75, 9 ± 241
Baptisia tinctoria (L.) R. Br. ex Ait. f.		0	0.14, 0.4 ± 6	0
Desmodium cuspidatum (Muhl. ex Willd.) DC. ex Loud.		0.09, 1 ± 34	0.14, 1 ± 41	0
Lathyrus palustris L.		0.27, 1 ± 51	0	0
Lespedeza procumbens Michx.		0	0	0.25, 0.05 ± 0.05

Continued on next page

Table 1.1, continued

Lotus corniculatus L.		0	0.14, 0.4 ± 6	0
Medicago lupulina L.		0	0.14, 0.03 ± 0.03	0
Melilotus alba Medikus		0.09, 0.02 ± 0.02	0	0
Melilotus officinalis (L.) Lam.		0	0.14, 0.06 ± 0.06	0
Trifolium campestre Schreb.		0.09, 0.02 ± 0.02	0	0
Trifolium dubium Sibthorp		0	0	0.25, 0.05 ± 0.05
* *Trifolium incarnatum* L.	Lackney 1981	N/A	N/A	N/A
Trifolium pretense L.		0.09, 0.7 ± 26	0	0.25, 3 ± 80
Trifolium repens L.		0.09, 0.02 ± 0.02	0.14, 0.03 ± 0.03	0
Fagaceae				
Quercus macrocarpa Michx.		0.09, 0.02 ± 0.02	0.14, 0.03 ± 0.03	0
Quercus rubra L.		0.09, 0.3 ± 4	0	0
Gentianaceae				
Gentiana andrewsii Griseb.	Macior 1969	N/A	N/A	N/A
Gentiana clausa Raf.		0.09, 0.7 ± 26	0.14, 2 ± 46	0
Gentiana puberulenta J. Pringle		0.09, 0.02 ± 0.02	0	0
Gentianopsis crinita (Froel.) Ma		0	0.14, 1 ± 41	0
Gentianopsis virgata (Raf.) Holub		0.09, 0.02 ± 0.02	0	0
Grossulariaceae				
Ribes americanum P. Mill.		0.18, 0.3 ± 4	0.14, 1 ± 41	0
Hamamelidaceae				
Liquidambar styraciflua L.		0	0	0.25, 0.05 ± 0.05

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Table 1.1, continued

Hydrophyllaceae				
Hydrophyllum appendiculatum Michx.		0	0.14, 1 ± 41	0
Iridaceae				
Iris pseudacorus L.	Farnsworth et al. 2007	N/A	N/A	N/A
Iris versicolor L.		0.18, 3 ± 101	0	0
* *Iris virginica* L.	Piehl 1965	N/A	N/A	N/A
Juncaceae				
Juncus brevicaudatus (Engelm.) Fern.		0	0.14, 0.4 ± 6	0
Juncus canadensis J. Gay ex Laharpe		0.09, 0.7 ± 26	0	0
* *Juncus effusus* L.	Foster 2003, Farnsworth et al. 2007	0.09, 0.7 ± 26	0.14, 1 ± 41	0.75, 6 ± 196
Juncus nodosus L.		0.36, 2 ± 55	0.71, 12 ± 297	0
Juncus tenuis Willd.	Farnsworth et al. 2007	0.09, 0.3 ± 4	0.14, 3 ± 116	0
Juncaginaceae				
Triglochin maritima		0.09, 0.02 ± 0.02	0	0
Lamiaceae				
Clinopodium vulgare L.		0	0.14, 0.03 ± 0.03	0.25, 2 ± 72
Glechoma hederacea L.		0	0.14, 0.03 ± 0.03	0
Lycopus americanus Muhl. ex W. Bart.		0.64, 3 ± 99	0.29, 0.06 ± 0.06	0
Lycopus uniflorus Michx.	Farnsworth et al. 2007	0.91, 10 ± 258	0.86, 11 ± 271	0.75, 6 ± 196
Mentha aquatica L.		0.09, 0.02 ± 0.02	0	0
Mentha arvensis L.	Farnsworth et al. 2007	0.09, 0.04 ± 0.04	0	0
Monarda media Willd.		0.09, 0.5 ± 8	0	0
Prunella vulgaris L.	Macior 1969	0.45, 4 ± 127	0.86, 12 ± 244	0.50, 0.2 ± 0.2
Pycnanthemum tenuifolium Schrad.		0.18, 0.7 ± 26	0	0

Continued on next page

Table 1.1, continued

* *Pycnanthemum virginianum* (L.) T. Dur. & B.D. Jackson ex B.L. Robins. & Fern.	Piehl 1965	0.27, 3 ± 103	0.29, 3 ± 85	0.25, 0.1 ± 0.1
Scutellaria galericulata L.		0.09, 1 ± 52	0	0
Scutellaria lateriflora L.	Farnsworth et al. 2007	0.18, 0.07 ± 0.07	0.14, 0.03 ± 0.03	0
Liliaceae				
Maianthemum canadense Desf.		0.09, 0.7 ± 26	0	0
Maianthemum racemosum ssp. *racemosum* (L.) Link		0.09, 1 ± 52	0	0
Lythraceae				
Decodon verticillatus (L.) Ell.		0	0.14, 1 ± 41	0
Lythrum alatum Pursh		0.18, 0.7 ± 26	0	0
Lythrum salicaria L.		0	0.28, 4 ± 260	0
Malvaceae				
Hibiscus moscheutos ssp. *moscheutos* L.		0	0	0.25, 2 ± 72
Myricaceae				
Myrica gale L.		0	0.14, 0.4 ± 6	0
Oleaceae				
Fraxinus pennsylvanica Marsh.		0	0.43, 3 ± 116	0.25, 3 ± 80
Ligustrum vulgare L.		0	0	0.25, 0.8 ± 11
Onagraceae				
Circaea lutetiana ssp. *Canadensis* (L.) Aschers. & Magnus		0.09, 0.04 ± 0.04	0	0
Epilobium coloratum Biehler	Farnsworth et al. 2007	0	0	0.25, 0.8 ± 11
Epilobium leptophyllum Raf.		0.09, 0.02 ± 0.02	0	0
Epilobium strictum Muhl. ex Spreng.		0	0.29, 0.1 ± 0.1	0
Ludiwigia alternifolia L.		0	0	0.25, 2 ± 21

Continued on next page

Table 1.1, continued

Oxalidaceae				
Oxalis corniculata L.		0	0.14, 1 ± 41	0
Oxalis stricta L.		0.09, 0.02 ± 0.02	0.14, 3 ± 89	0.50, 4 ± 136
Pinaceae				
Larix laricina (Du Roi) K. Koch		0	0.14, 1 ± 41	0
Pinus strobus L.	Farnsworth et al. 2007	0.09, 0.3 ± 4	0	0
Plantaginaceae				
Plantago lanceolata L.		0	0.43, 2 ± 52	0
Plantago major L.		0	0.43, 2 ± 80	0
Plantago rugelii Dcne.		0.27, 1 ± 30	0.14, 1 ± 41	0
Poaceae				
Agrostis capillaris L.		0	0.29, 5 ± 181	0.25, 2 ± 72
Agrostis gigantea Roth		0.55, 5 ± 129	0.29, 2 ± 80	0.25, 4 ± 137
Agrostis stolonifera L.		0	0.14, 2 ± 52	0.25, 4 ± 137
Alopecurus carolinianus Walt.		0	0	0.25, 2 ± 21
Bromus inermis Leyss.	Farnsworth et al. 2007	N/A	N/A	N/A
Cinna arundinacea L.	Farnsworth et al. 2007	N/A	N/A	N/A
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes		0.09, 0.7 ± 26	0	0
Deschampsia caespitosa (L.) Beauv.		0.09, 2 ± 58	0.14, 1 ± 41	0
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark		0	0.29, 3 ± 116	0
Dichanthelium clandestinum (L.) Gould		0	0.29, 2 ± 80	0.50, 4 ± 94
Dichanthelium dichotomum var. *dichotomum* (L.) Gould		0	0.14, 1 ± 41	0

Continued on next page

Table 1.1, continued

Dichanthelium leucothrix (Nash) Freckmann		0	0	0.25, 6 ± 194
Dichanthelium villosissimum (Nash) Freckmann		0.09, 0.3 ± 4	0	0
Echinochloa muricata (Beauv.) Fern.	Farnsworth et al. 2007	N/A	N/A	N/A
Elymus riparius Wieg.		0.09, 0.7 ± 26	0.14, 3 ± 85	0
Elymus trachycaulus (Link) Gould ex Shinners		0.09, 0.02 ± 0.02	0	0
Glyceria canadensis (Michx.) Trin.		0.09, 0.7 ± 26	0	0
Glyceria grandis S. Wats.	Farnsworth et al. 2007	N/A	N/A	N/A
Glyceria septentrionalis A.S. Hitchc.		0	0	0.25, 2 ± 21
Glyceria striata (Lam.) A.S. Hitchc.		0	0.14, 1 ± 41	0
Leersia oryzoides (L.) Sw.	Farnsworth et al. 2007	0	0	0.25, 3 ± 80
Microstegium vimineum (Trin.) A. Camus		0	0.14, 7 ± 461	0
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi		0.09, 1 ± 52	0.14, 0.03 ± 0.03	0
Panicum flexile (Gattinger) Scribn.		0	0	0.75, 9 ± 241
Paspalum dilatatum Poir.		0	0	0.50, 8 ± 243
* *Phalaris arundinacea* L.	Foster 2003, Farnsworth et al. 2007	0.45, 7 ± 272	0.29, 3 ± 92	0
Phleum pratense L.		0	0.57, 5 ± 153	0
Poa pratensis L.		0.55, 5 ± 165	0.29, 2 ± 52	0.25, 3 ± 80
Schizachyrium scoparium (Michx.) Nash		0.09, 0.7 ± 26	0	0

Continued on next page

Table 1.1, continued

Spartina pectinata Bosc ex Link		0.09, 1 ± 52	0	0
* *Triticum aestivum* L.	Lackney 1981	N/A	N/A	N/A
Polygonaceae				
* *Polygonum amphibium* L.	Piehl 1965	N/A	N/A	N/A
Polygonum cespitosum Blume		0	0	0.25, 6 ± 261
Polygonum hydropiper L.		0.27, 3 ± 121	0	0
Polygonum sagittatum L.	Farnsworth et al. 2007	0.09, 2 ± 76	0.29, 4 ± 150	0.25, 3 ± 80
Polygonum virginianum L.		0	0	0.25, 0.05 ± 0.05
Rumex crispus L.		0.09, 0.5 ± 8	0	0
Primulaceae				
Lysimachia ciliata L.	Farnsworth et al. 2007	0.09, 0.7 ± 26	0.14, 3 ± 92	0
Lysimachia terrestris (L.) B.S.P	Farnsworth et al. 2007	N/A	N/A	N/A
* *Lysimachia quadrifolia* L.	Piehl 1965	N/A	N/A	N/A
Ranunculaceae				
Caltha palustris L.		0.18, 1 ± 33	0.43, 9 ± 297	0.25, 2 ± 30
* *Clematis virginiana* L.	Foster 2003, Farnsworth et al. 2007	0	0.14, 1 ± 41	0.75, 9 ± 241
Ranunculus acris L.		0	0.71, 6 ± 181	0
* *Ranunculus hispidus* Michx.	Piehl 1965	N/A	N/A	N/A
Ranunculus sp.	Farnsworth et al. 2007	N/A	N/A	N/A
* *Thalictrum dasycarpum* Fisch. & Avé-Lall.	Piehl 1965	N/A	N/A	N/A
Thalictrum dioicum L.		0.18, 0.7 ± 26	0.14, 1 ± 41	0
Thalictrum pubescens Pursh	Farnsworth et al. 2007	0.27, 4 ± 151	0.57, 3 ± 88	0

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Table 1.1, continued

Rhamnaceae				
* *Rhamnus frangula* L.	Piehl 1965, Farnsworth et al. 2007	0.45, 7 ± 209	0.29, 0.06 ± 0.06	0
Rosaceae				
Agrimonia parviflora Ait.		0	0.14, 1 ± 41	0.50, 2 ± 21
Argentina anserine (L.) Rydb.		0.09, 3 ± 120	0	0
Dasiphora floribunda (Pursh) Kartesz, comb. nov. ined.		0.27, 5 ± 129	0.14, 4 ± 120	0
Filipendula rubra (Hill) B.L. Robins.		0.09, 0.02 ± 0.02	0	0
Fragaria vesca L.		0.09, 0.7 ± 26	0.14, 1 ± 41	0
Fragaria virginiana Duschesne		0.18, 1 ± 33	0	0
Geum aleppicum Jacq.		0.09, 0.02 ± 0.02	0.14, 0.03 ± 0.03	0.25, 0.05 ± 0.05
Geum rivale L.		0.18, 1 ± 51	0.14, 0.03 ± 0.03	0
Geum sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Potentilla norvegica L.		0	0.29, 1 ± 41	0
Potentilla simplex Michx.	Farnsworth et al. 2007	0.09, 1 ± 30	0.29, 4 ± 120	0.50, 3 ± 80
Prunus serotina Ehrh.		0.09, 0.3 ± 4	0	0
Rosa carolina L.		0.09, 1 ± 30	0	0
Rosa multiflora Thunb. ex Murr.	Farnsworth et al. 2007	0	0.29, 1 ± 41	0
Rosa virginiana P. Mill.		0.09, 0.7 ± 26	0	0.50, 6 ± 149
Rubus allegheniensis Porter		0.09, 1 ± 52	0	0.50, 9 ± 241
Rubus idaeus L.		0.09, 0.7 ± 26	0.14, 1 ± 41	0
Rubus hispidus L.		0	0.14, 2 ± 80	0
Rubus pubescens Raf.		0	0.14, 0.4 ± 6	0
Rubus sp.	Farnsworth et al. 2007	N/A	N/A	N/A

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Table 1.1, continued

Spiraea alba Du Roi		0	0.14, 1 ± 41	0
Spiraea tomentosa L.	Farnsworth et al. 2007	0	0.14, 0.4 ± 6	0
Rubiaceae				
Diodia teres Walt.		0	0	0.25, 2 ± 72
Galium aparine L.		0	0.57, 2 ± 79	0.25, 0.1 ± 0.1
Galium palustre L.		0.09, 0.04 ± 0.04	0.14, 1 ± 41	0
Galium tinctorium L.		0	0	0.25, 0.05 ± 0.05
Galium trifidum L.		0.09, 0.02 ± 0.02	0	0
Galium sp.	Farnsworth et al. 2007	N/A	N/A	N/A
Salicaceae				
Populus deltoides Bartr. ex Marsh.		0	0.14, 1 ± 41	0
Populus grandidentata Michx.		0.09, 0.02 ± 0.02	0	0
Populus tremuloides Michx.		0.09, 0.7 ± 26	0.14, 0.03 ± 0.03	0
Salix bicolor Fries		0.09, 0.3 ± 4	0	0
Salix discolor Muhl.		0.18, 0.8 ± 12	0.57, 6 ± 157	0
Salix sericea Marsh.		0.09, 0.7 ± 26	0	0
Saxifragaceae				
Parnassia glauca Raf.		0.27, 3 ± 81	0.29, 4 ± 123	0
Saxifraga pensylvanica L.		0.09, 0.04 ± 0.04	0	0
Scrophulariaceae				
Agalinas paupercula var. *paupercula* (Gray) Britt.		0.09, 0.02 ± 0.02	0	0
* *Chelone glabra* L.	Piehl 1965, Foster 2003, Farnsworth et al. 2007	0	0	0.25, 2 ± 72

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Table 1.1, continued

Chelone lyonii Pursh		0	0.14, 0.03 ± 0.03	0
Gratiola aurea Pursh		0.09, 2 ± 55	0	0
Mimulus ringens L.	Farnsworth et al. 2007	N/A	N/A	N/A
Smilacaceae				
Smilax herbacea L.		0	0.14, 2 ± 80	0
Solanaceae				
Solanum carolinense L.		0	0	0.75, 3 ± 80
Solanum dulcamara L.	Farnsworth et al. 2007	0	0.14, 0.03 ± 0.03	0
Sparganiaceae				
Sparganium andocladum (Engelm.) Morong		0	0	0.25, 2 ± 21
Thelypteridaceae				
* *Thelypteris palustris* Schott	Piehl 1965	0	0.71, 8 ± 185	0
Typhaceae				
Typha angustifolia L.		0	0.14, 1 ± 18	0
* *Typha latifolia* L.	Piehl 1965	0.09, 0.7 ± 26	0.14, 0.03 ± 0.03	0
Ulmaceae				
Ulmus rubra Muhl.		0.09, 0.7 ± 26	0	0
Urticaceae				
Boehmeria cylindrica (L.) Sw.	Farnsworth et al. 2007	0.09, 0.7 ± 26	0	0.50, 8 ± 242
Pilea pumila (L.) Gray		0.09, 0.6 ± 8	0.14, 0.03 ± 0.03	0
Verbenaceae				
* *Verbena hastata* L.	Piehl 1965, Farnsworth et al. 2007	N/A	N/A	
Verbena urticifolia L.		0	0.14, 0.5 ± 6	0
Vitaceae				
Parthenocissus quinquefolia (L.) Planch.		0	0.29, 0.5 ± 6	0
Vitis labrusca L.		0	0.14, 2 ± 47	0.25, 5 ± 142
Vitis riparia Michx.		0.18, 0.7 ± 26	0.29, 0.06 ± 0.06	0

Table 1.2. A summary of statistical results from the ANOVA models testing for effects of sub-region (Northeast, Southeast, or Midwest) nested within region (core or edge) on the percent cover of (A) natives, (B) non-native invasives, (C) non-native non-invasive, and (D) species with native and non-native genotypes associated with *P. lanceolata*.

Effect	df	M.S.	*F*	*P*
A. Natives:				
Region	1	0.0400	3.3947	0.08194
Sub-region	2	0.0251	2.1269	0.1482
Residuals	18	0.0118		
B. Non-native invasives:				
Region	1	0.0020	0.0108	0.9183
Sub-region	2	0.0508	2.8129	0.0865
Residuals	18	0.0181		
C. Non-native non-invasives				
Region	1	0.0631	3.7076	0.0701
Sub-region	2	0.0132	0.7756	0.47522
Residuals	18	0.0170		
D. Native and non-native genotypes:				
Region	1	0.0010	0.7661	0.3930
Sub-region	2	0.0212	1.6266	0.2242
Residuals	18	0.0130		

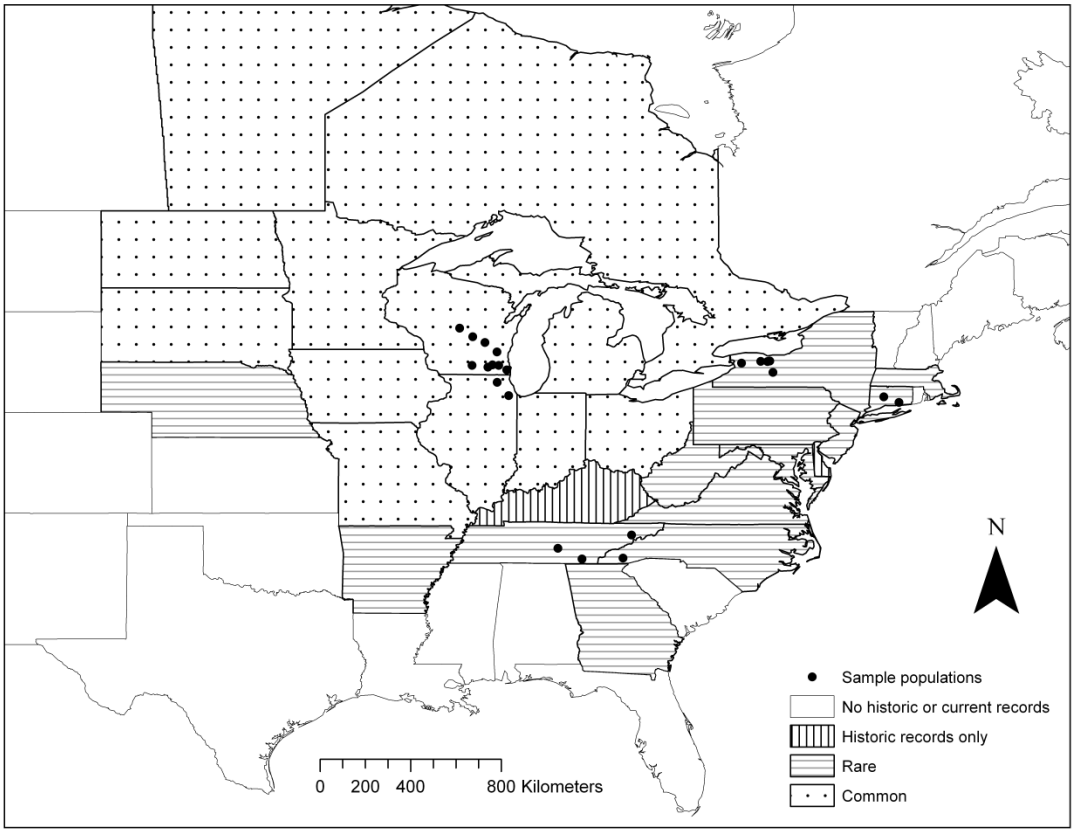

Figure 1.1. Range map of *Pedicularis lanceolata*'s global distribution showing locations of sample populations. Status reflects the state (USA) or provincial (Canada) rank of *P. lanceolata* as a species of conservation concern. A status of "common" refers to apparently secure (S4) or not ranked. A status of rare refers to critically imperiled (S1), imperiled (S2), or vulnerable (S3) (NatureServe 2009).

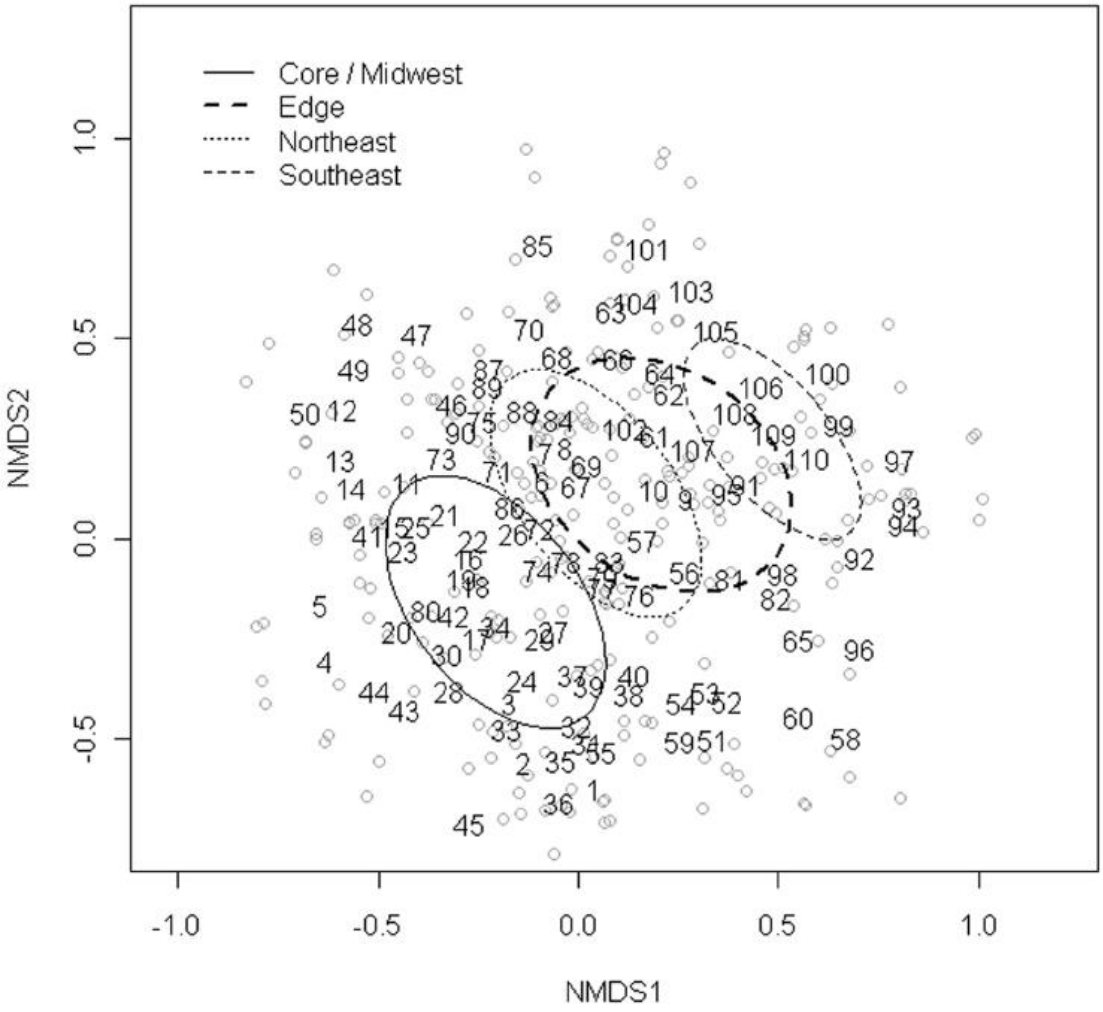

Figure 1.2. Ordination projection of all associated species encountered generated using Nonmetric Multidimensional Scaling. Species are open circles, and numbers are plots within sites. Ellipses depict the standard deviations of point scores from the covariance matrix for each region. Midwestern plots are on the left, Northeastern plots are in the center, and Southeastern plots are on the right. Numbers corresponding to plots are: Midwest 1-55, Northeast 56-90, and Southeast 91-110.

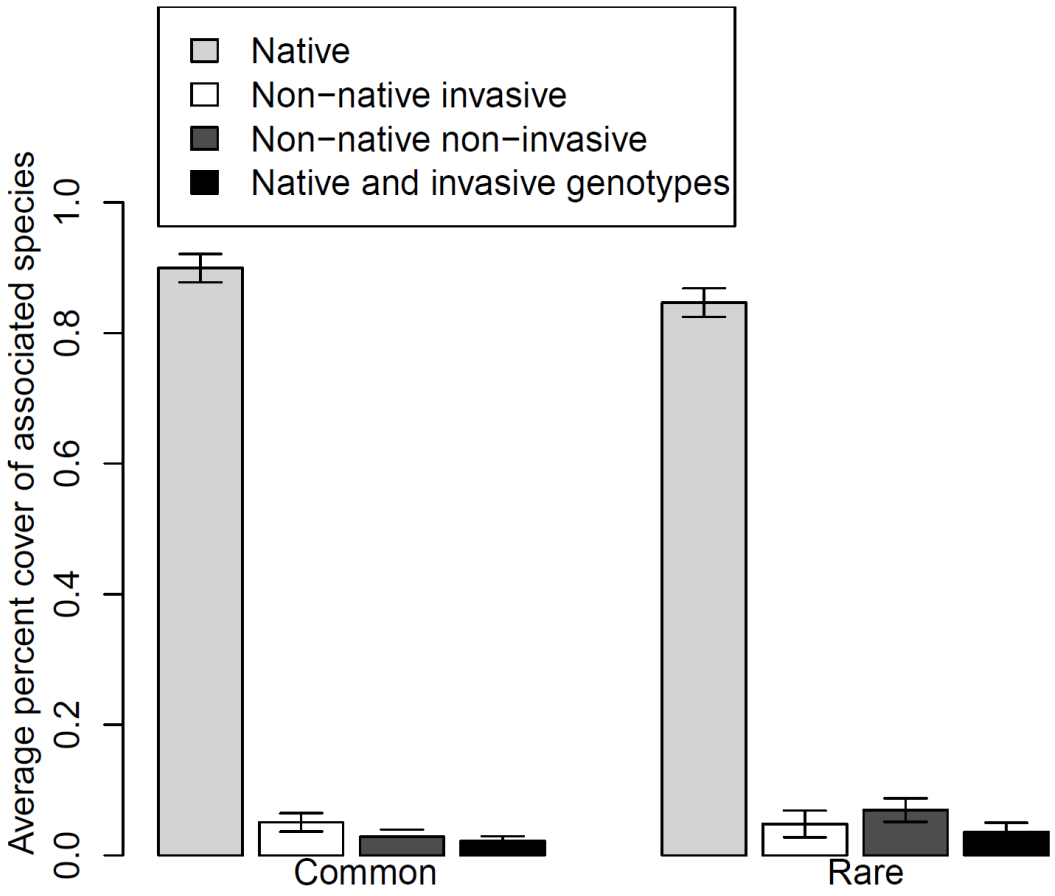

Figure 1.3. Average relative abundance in percent covers of natives, non-native invasives, non-native non-invasives, and species with native and non-native genotypes of *P. lanceolata* in Midwestern populations where the species is common and eastern population where the species is rare. Error bars show one standard error of the mean.

CHAPTER II

FACILITATIVE AND COMPETITIVE INTERACTIONS BETWEEN A ROOT HEMIPARASITE, *PEDICULARIS LANCEOLATA*, AND ITS NATIVE NON-INVASIVE AND NON-NATIVE INVASIVE HOSTS

Abstract

The eradication of non-native invasive species may have negative indirect effects on native species if there are facilitative interactions between the non-native invasive and native organisms. For native hemiparasitic plants, the removal of non-native invasive species serving as host plants could be detrimental if positive interactions resulting from root connections between hemiparasite and host outweigh negative interactions due to aboveground competition.

To compare the costs of aboveground competition versus belowground facilitative effects of native non-invasive ("native") versus non-native invasive ("invasive") hosts on the native hemiparasite, *Pedicularis lanceolata*, this species was grown in a greenhouse with only natives, with a mixture of native and invasive plants, and with invasives alone in the absence or presence of above-ground competition for light simulated by clipping hosts or not clipping them. In addition, a field experiment was performed in which natives, non-natives, both natives and non-natives, or no hosts (control treatment) were clipped and removed for two growing seasons from around focal *P. lanceolata* plots.

Over-winter survival, total biomass, total number of haustoria produced per pot, and number of inflorescences of *P. lanceolata* all were significantly greater when it was grown with native hosts regardless of the presence or absence of above-ground competition. *Pedicularis lanceolata* did not flower when grown with invasive plants

alone regardless of clipping treatment or with a mixture of clipped native and invasive plants. Flowers were, however, produced by *P. lanceolata* when it was grown with a mixture of unclipped native and invasive plants or native plants only regardless of clipping treatment. In the field, removal of all neighboring plants had detrimental effects on the growth and survival of *P. lanceolata*, but the effects of removing native and non-native plants were variable because woody native plants were also strong competitors for light with *P. lanceolata*.

The greenhouse results suggest that the effects of invasive species on hemiparasite performance may be due to disrupted facilitations between the hemiparasite and its more preferred native host plants. However, if native associated species are strong competitors for light, then any potential facilitative interactions may not outweigh the costs of negative competitive interactions.

Introduction

Non-native invasive species (henceforth "invasives") are considered a significant threat to native species because of their abilities to alter ecosystem function and community structure (*e.g*, D'Antonio and Vitousek 1992, Sanders *et al.* 2003, Crowl *et al.* 2008). Although there have been a number of instances in which the eradication of invasive species has been successful (Tershy *et al.* 2002, Anderson 2004, Donlan *et al.* 2007), there is concern about indirect negative effects of removing invasive species on ecosystem processes and native biota (El-Ghareeb 1991, Bergstrom *et al.* 2009, among many others). Focusing on competitive interactions between invasive and native species also may overlook important interactions, such as facilitations, and result in unintended negative indirect effects of invasive species removal. For instance, the removal of

invasive vegetation that supplies food or creates habitat may have negative effects on native fauna (Schiffman 1994, DeLoach 1996). Similarly, the removal of invasive species growing with a parasitic plant has the potential to negatively affect the parasite if the invasive species serve as facultative host plants. Alternatively, if the invasive species disrupts the ability of the parasite to use more beneficial native hosts, then the removal of the invasive species could be beneficial.

Parasitic plants may be wholly parasitic (unable to photosynthesize and completely dependent upon host plants) or hemiparasitic (able to photosynthesize but reliant on host plants for additional mineral nutrients and water to complete their life cycle) (Heide-Jørgensen 2008). Hemiparasitic plants comprise the majority of the nearly 4500 parasitic plants in the world (Heide-Jørgensen 2008) and have life history traits associated with elevated rates of extinction (*e.g* transient seed banks, dependence on multiple pollinator visits to set seed) (Bekker and Kwak 2005), so understanding the potential for negative effects of invasive species eradications on hemiparasites is also of significant conservation and management interest.

For hemiparasites, the affinity for any particular host plant depends on the balance between competitive aboveground interactions and facilitative belowground interactions (Atsatt and Strong 1970). By separately manipulating aboveground competition between two root hemiparasites, *Odontites rubra* (Baumg.) and *Rhinanthus serotinus* (Schönh.), and the host plant *Medicago sativa* L., Matthies (1995) documented net negative effects of aboveground competition on the growth and fruit production of the two hemiparasites despite facilitative belowground interactions between *M. sativa* and these two hemiparasites. This evidence suggests that competitive invasive hosts that form dense

monocultures may be poor host plants for native hemiparasites if the negative effects of aboveground competition for light outweigh the positive effects of belowground facilitative interactions.

Although many studies have investigated host preferences of hemiparasites for native hosts (*e.g* Gibson and Watkinson 1991, Svensson and Carlsson 2004, Lawrence and Kaye 2008), studies comparing preferences of hemiparasites for native versus invasive hosts are scant and have reached different conclusions on the effects of invasive hosts on hemiparasites (Fellows and Zedler 2005, Prider *et al.* 2009). Therefore, to investigate the effects of native versus invasive hosts on hemiparasite survival, growth, and reproduction, and possible mechanisms behind these effects, I grew *Pedicularis lanceolata* Michx. (Orobanchaceae), a root hemiparasitic plant, with host arrays of native plants only, a mixture of native and invasive plants, and invasive plants only. These three host types (native, mixed, and invasive) served as proxies for different times in the invasion process because the biological effects of invasive hosts on hemiparasites may depend on whether or not they have surpassed a lag time to form a monoculture.

In addition, the three host type treatments were crossed with a clipping treatment to determine if there were aboveground competitive effects of any of these hosts on *P. lanceolata*. This treatment also allowed me to determine the magnitude of the effects of aboveground competition as a mechanism for any differences between native and invasive hosts. In this treatment, clipped hosts interacted with *P. lanceolata* only facilitatively belowground whereas unclipped hosts simultaneoulsy interacted with *P. lanceolata* competitively aboveground and facilitatively belowground. If *P. lanceolata* performs worse when growing with unclipped invasive hosts than when growing with

clipped invasive hosts, I can conclude that aboveground competition is a plausible mechanism for observed negative effects of invasive hosts. Alternatively, if *P. lanceolata* grows equally well with unclipped or clipped invasive hosts, then another mechanism (*e.g* the "pseudo-host" effect; Fellows and Zedler 2005) would better explain any observed negative effects of invasive hosts on *P. lanceolata. Pedicularis lanceolata* is an ideal species with which to test the effects of native and invasive hosts because it is a generalist hemiparasitic species (Piehl 1965) that cannot live longer than three months without a host (Lackney 1981). This species also is regionally rare in North America (Brumback *et al.* 1996, NatureServe 2009), so insights gained from this study will contribute directly to its management (Allard 2001).

Methods

Study species

Pedicularis lanceolata is a short-lived perennial that grows in a variety of wet habitats such as swamps, wet meadows, and streamsides (Allard 2001). It is an outcrossing species that flowers late in the growing season (August to September) and is mainly pollinated by bumblebees (*Bombus* spp.) (Macior 1969). The documented range of *P. lanceolata* extends from Massachusetts to Georgia on the east coast of the United States and westward in North America into Missouri and Manitoba, Canada (NatureServe 2009). *Pedicularis lanceolata* is common in the Midwestern United States and all of central and eastern Canada, but many states along the eastern coast of the United States list it as rare and of conservation concern (*i.e.*, Endangered, Threatened, or a Species of Concern) (Brumback *et al.* 1996, NatureServe 2009). *Pedicularis lanceolata* is a generalist root hemiparasite that parasitizes many host plants including graminoids, ferns,

forbs, and woody shrubs (Piehl 1965, Lackney 1981, Foster 2003). Specialized cup-like structures on the roots of *P. lanceolata* called haustoria allow for the flow of water and nutrients from the host to the hemiparasite (Heide-Jørgensen 2008). On average, haustoria of *P. lanceolata* are 1.5 mm in their longest dimension (Piehl 1965).

Greenhouse experiment

To compare *P. lanceolata* survival, growth, and haustoria production when grown with different host types and in the presence or absence of aboveground competition with these hosts, I conducted a factorial greenhouse experiment with three levels of host types (native, mixed, and invasive) and two clipping treatments (clipped or unclipped hosts). All host plant arrays were planted into 3.7 L pots containing a 2:1 mixture of loam and peat in the first week of October 2007 and randomly assigned to benches in a climate controlled greenhouse (summer: 25°C daytime, 15°C nighttime, 80% humidity; winter:15°C daytime, 10°C nighttime, 80% humidity) at Harvard Forest in Petersham, Massachusetts. Each replicate consisted of a pot with one randomly assigned individual *P. lanceolata* and two host plants. Roots and shoots of hosts were cut to equal sizes at the time of planting to minimize differences in initial above- and belowground biomasses between hosts. Within each pot, hosts were planted 10 cm apart with enough room to allow for *P. lanceolata* to later be planted in, so that all three plants would be 10 cm apart from one another.

Two native species (*Juncus effusus* L. and *Scirpus cyperinus* (L.) Kunth) and two invasive species (*Bromus inermis* Leyss. and *Phalaris arundinacea* L.) were used in the host arrays for the three levels of host type (Table 2.1). These four host species were chosen because all of them, with the exception of *B. inermis*, had been previously

documented as hosts of *P. lanceolata* (Foster 2003), all four are common associated species of *P. lanceolata* throughout its range (Chapter I), and graminoids have been recorded as the predominant hosts of *P. lanceolata* in field excavations in Michigan (Piehl 1965). Although individual states within *P. lanceolata*'s range disagree on the degree of invasiveness of *B. inermis* and *P. arundinacea* (USDA 2009), both of these species have been documented as being highly competitive and capable of excluding native plants (Wilson 1989, Green & Galatowitsch 2002). New England Wetland Plants of Amherst, Massachusetts, USA provided the native host plants, whereas invasive hosts were collected in the field in September of 2007 from populations in which they were growing dominant in monocultures. *Bromus inermis* was collected from a population in Southampton, Massachusetts (42°13'26" N, 72°40'41"W), and *P. arundinacea* was collected from a population in Amherst, Massachusetts (42°23'6"N, 72°32'12"W).

Attempts to grow *P. lanceolata* from seed supplied by Prairie Moon Nursery, Winona, Minnesota using a variety of cues to break dormancy (*e.g.*, exposure to giberellic acid, scarification with sandpaper, or 3 months of cold moist stratification) were unsuccessful from the fall of 2007 to the spring of 2008. Thus, *P. lanceolata* seedlings were collected from two populations near Ann Arbor, Michigan in the second week of June 2008 (Barton Pond: 42°18'26" N, 83°36'42"; and Highland: 42°15'17" N, 83°36'42" W). Equal numbers of seedlings from the two source populations were transplanted randomly into pots of the clipping and host type treatments to minimize differences between source population and the experimental treatments of interest. Seedling age was confirmed by the presence of cotyledons. Transplant shock and seedling mortality was high (55%), so new seedlings were transplanted once a week as

needed from the end of June through early August 2008, by which time all 240 pots contained established seedlings. Records on the transplant dates for each pot were kept to include as a covariate in the statistical analysis of the experiment because time of attachment is sometimes an important predictor of hemiparasite fitness as measured by seed set (Svensson & Carlsson 2004). Heights of *P. lanceolata* were recorded at the time of transplanting to include initial size as a covariate in the final analysis.

In the "clipped" treatment, the shoots of both hosts were trimmed to a height of 3 cm once every ten days throughout the growing season so that *P. lanceolata* and its hosts only interacted belowground. In the control, "unclipped" treatment, the shoots of all host plants were left unmanipulated, so that *P. lanceolata* interacted both aboveground and belowground with its hosts. There were 12 replicates per host species combination for each clipping treatment for a total sample size of 240 pots (12 replicates × 2 clipping treatments × 10 host species combinations = 240 pots). Clipping treatments began in May 2008 and continued through the end of the experiment in August 2009. Locations of pots were randomized at the beginning and middle of each growing season in 2008 and 2009 to prevent differences due to the placement of plants within the greenhouse.

Over-winter survival of *P. lanceolata* seedlings was recorded in May 2009. Pots in which *P. lanceolata* did not survive the winter were removed from the experiment at the end of May 2009. Half of the remaining pots were harvested in the third week of June 2009, and the other half of the remaining pots were harvested in the second week of August 2009. Two harvests were performed to document any phenological differences in haustoria formation. Before the August harvest, the number of inflorescences on each *P. lanceolata* was recorded. At this time, most of the reproductive *P. lanceolata* had

produced buds and were flowering, but the flowering time of *P. lanceolata* in the field continues into September. Thus, the August flower measurements are conservative estimates of flower production.

During each harvest, the above- and belowground plant material of each species was separated. Belowground material was separated from soil by spraying water on roots over a 0.25 mm sieve. Roots of the different species were separated based on differences in their color and morphology: *B. inermis* roots were pale yellow, *P. arundinacea* roots were whitish-pink with constrictions, *P. lanceolata* roots were stark white, *S. cyperinus* roots were brown and fibrous, and *J. effusus* roots were dark red and fibrous. Haustoria on *P. lanceolata* and hosts were counted by examining hydrated belowground plant material under a dissecting microscope. Above- and belowground plant material was dried in an oven at 70°C for 72 hours until constant weight then weighed (±0.005 g).

Greenhouse statistical analyses

A generalized linear model (glm) with a binomial error distribution (logit link) was used to test for differences in the survival of *P. lanceolata* from the fall of 2008 to the spring of 2009. Categorical predictor variables used were clipping treatment, host type, and *P. lanceolata* source population; *P. lanceolata* initial size and transplant date were entered as continuous covariates. A contingency table analysis was used to determine if winter mortality of *P. lanceolata* differed among treatments. Generalized linear models were also used to analyze the responses of *P. lanceolata* ln(total biomass) (Gaussian link), counts of the total number of haustoria per pot (Poisson link), and number of inflorescences produced at the second harvest (Poisson link). Categorical

predictor variables were clipping treatment, host type, harvest, and *P. lanceolata* source population; *P. lanceolata* initial size, transplant date, and total host biomass were continuous covariates.

The primary objectives of this study were to determine the effects of host type, clipping, and a host type × clipping interaction on *P. lanceolata* performance. The interaction between host type and clipping was of interest from a management perspective where knowledge of how *P. lanceolata* performance might among host types and between clipping treatments would provide guidance for removals or maintenance of hosts around sensitive populations of *P. lanceolata*. Given the objectives of the study and the large number of possible interaction terms for the glm models that could lead to increased family-wise type I errors, for each glm all interactions except for the host type × clipping interaction were left out of the model (exclusion of the other interactions did not change the magnitudes of the effect sizes of the main effects (*e.g.*, host type, clipping, *P. lanceolata* source, etc.) or host type × clipping interaction). Post-hoc pairwise comparisons among the three host types were carried out using Tukey's honest significant differences (HSD) test.

Most of the predictor variables are clearly fixed effects, but source population of *P. lanceolata* could be considered a random effect. Non-normal data with fixed and random effects are typically modeled with generalized linear mixed models (Gotelli and Ellison 2004). However, in a recent paper Bolker *et al.* (2009) describe issues that statisticians have in estimating the parameters for such models and outline instances where procedures in standard statistical software used by many ecologists (*e.g*, SAS and R) may provide spurious *P* values. Given the issues associated with non-normal data and

glm's, all predictor variables in glm's with non-normal error distributions were treated as fixed effects. All statistical analyses were performed using R statistical software version 2.8.2 (R Development Core Team 2009).

Field removal experiment

In 2008 and 2009 I performed removal experiments where invasive and non-invasive non-native plants were present on twelve 1m × 1m plots that had reproductive adult *P. lanceolata* individuals in their centers. The sample size in this experiment was limited by low numbers of reproductive plants, risks associated with removing host plants, and the guidelines of state permits to study the plants. There were four removal treatments (a disturbance control, removal of non-natives, removal of natives, and removal of all plants except *P. lanceolata*) with three replicates per treatment. In the removal plots, I clipped either all invasive and non-native plants, all natives, or all plants except for *P. lanceolata* every ten days throughout the growing season and removed all leaf litter. In the disturbance control, litter was removed but no plants were clipped. Three of the four treatments represented possible management scenarios: no management action (control treatment), selective clipping of non-native plants, and non-selective removal of all surrounding plants. The non-selective management treatment could occur with spraying of herbicide or mowing before *P. lanceolata* emerges in late winter or early spring. Within the central 50 × 50 cm of each plot I recorded the stem length and number of flowers produced by *P. lanceolata* in late August at the time of flowering. Pre-treatment data were collected in August of 2007, and post-treatment data were collected in 2008 and 2009. I recorded information only on plants in the central 50 × 50 cm of the plot to control for edge effects of shading by, or host use of, neighboring plants outside of

the removal plot. Because the plots were all placed in invaded areas, to confirm that any increases in *P. lanceolata* growth and survival were due to the removal of non-natives or natives rather than due to the removal of sheer biomass, all plant material that was removed was dried and weighed to include as a covariate. Given the small sample size for this study due to the logistical constraints of studying a rare species, I examined the data graphically rather than performing formal statistical tests.

Results

Greenhouse experiment

In total, 80 *P. lanceolata* seedlings did not survive the winter of 2009, but a significantly higher proportion of *P. lanceolata* seedlings survived in pots planted with native or mixed hosts (79% and 76%, respectively) relative to seedlings in pots planted with only invasive hosts (53%: Fig. 2.1a; Table 2.2). Larger initial seedling size also significantly contributed to over-winter survival (Table 2.2). However, there were no effects of clipping treatment, source population, transplant date or the clipping treatment × host type interaction on *P. lanceolata* survival (Table 2.2). In the spring of 2009, a contingency table analysis showed that the distribution of surviving *P. lanceolata* from the two source populations did not differ between clipping treatments and host types (X^2 = 15.7, df = 27, P = 0.959).

Biomass of *P. lanceolata* in clipped treatments averaged 50% less than the *P. lanceolata* biomass in unclipped treatments (Table 2.2, Fig. 2.1b) and differed significantly among host types (Table 2.2). As with survival, the biomass of *P. lanceolata* planted with the three host types differed significantly: biomass was greatest in pots with native hosts alone and lowest in pots with only invasive hosts (Fig. 2.1b). The source

population of *P. lanceolata* seedlings had a marginally significant effect on *P. lanceolata* total biomass ($P = 0.051$; Table 2.2). The effects of *P. lanceolata* initial size, transplant date, harvest date, total host plant biomass and a clipping treatment × host type interactions did not significantly affect total *P. lanceolata* biomass (Table 2.2).

The total number of haustoria per pot for *P. lanceolata* in clipped treatments was on average less than half the total number of haustoria per pot in unclipped treatments (Table 2.2, Fig. 2.1c). Plants in pots planted with native hosts produced 53% more haustoria than plants in pots planted with invasive hosts and 39% more than plants in pots with mixed native and invasive hosts (Table 2.2, Fig. 2.1c). The source population of *P. lanceolata* seedlings and total host biomass also had significant effects on the total number of haustoria per pot, but the relationship between haustoria and host biomass alone was not strong ($F_{1,166} = 2.39$, $P = 0.124$, $R^2 = 0.0142$). There were no significant effects of *P. lanceolata* initial size, transplant date, harvest date or clipping treatment × host type interaction on haustoria production (Table 2.2).

Finally, *P. lanceolata* grown with invasive hosts, regardless of whether hosts were clipped or not, did not produce any inflorescences by the time of the second harvest (Fig. 2.1d). When grown with a mixture of native and invasive hosts, *P. lanceolata* did not produce flowers when hosts were clipped, but did produce inflorescences when hosts were not clipped. *Pedicularis lanceolata* grown only with native hosts produced flowers in both clipped and unclipped treatments. On average the number of inflorescences produced by *P. lanceolata* was three times greater for plants grown with unclipped native hosts compared to plants grown with clipped native hosts (Fig. 2.1d). Thus, the number of *P. lanceolata* flowers differed in response to host type and a clipping treatment × host

type interaction (Table 2.2). Clipping treatment, *Pedicularis lanceolata* source population, initial size, transplant date, and total host biomass did not influence the number of flowers produced by *P. lanceolata* (Table 2.2).

Field removal experiment

Species in removal plots were classified as native or non-native based on information from the USDA PLANTS Database (USDA 2009). Table 2.3 lists the species that were growing in the removal plots along with their origins (native or non-native). Some species with both non-native and native genotypes (*e.g., P. arundinacea*) were considered non-native in this study because they were dominant in their relative abundances within the plots. In both years there was no clear relationship between the amount of biomass removed from the plot and the percentage change in stem length of *P. lanceolata* in the center of the plot. The response of *P. lanceolata* growth to the treatments varied from year to year. Two of the three plots in which non-natives were removed showed higher stem growth between 2007 and 2008 compared to all other treatment plots (Fig. 2.2). However, in 2009 *P. lanceolata* growth was only greater in one of the non-native removal plots, and the largest increase in the percent change of stem of length of *P. lanceolata* was in a plot where natives were removed. In 2009, growth of *P. lanceolata* in plots where all surrounding plants was very low or none in plots where the *P. lanceolata* had died. Survival over the two years of the study was low in control treatments (mean probability of survival = 0.675) and in plots where all surrounding plants were removed (mean probability of survival = 0.6). Survival was higher in plots where either native (survival probability = 1) or non-native surrounding plants were removed (survival probability = 0.90).

Discussion

The co-occurrence of invasive plants with native hemiparasites poses unique challenges for conservation and management. The ability of many invasive plants to outcompete native plants for resources could make them ideal hosts for hemiparasites if facilitative parasitic interactions offset the cost of aboveground competition, or could make them poor hosts if competitive interactions outweigh facilitative interactions. The objective of this study was to investigate the balance between negative effects of aboveground competition and positive effects of belowground parasitism with native and invasive host plants on a native hemiparasite.

In the greenhouse, for all responses measured, *P. lanceolata* performed better with native hosts than with invasive hosts (Fig. 2.1). These results parallel findings of Fellows and Zedler (2005) who found that the endangered root hemiparasite *C. maritimus* ssp. *maritimus* Nutt. ex Benth. produced more flowers when grown with a native grass, *Distichlis spicata* L., than when grown with an invasive grass, *Parapholis incurva* (L.) C.E. Hubbard, in an outdoor pot experiment in California. In contrast, in a field experiment in Australia, Prider *et al.* (2009) found that photosynthetic and growth rates of a native stem hemiparasite *Cassytha pubescens* R. Br. were higher when it was attached to an invasive host, *Cytisus scoparius* (L.) Link than when it was growing with a native host, *Leptospermum myrsinoides* Schltdl. These differences in the effects of invasive and native hosts on hemiparasites across studies may be due to differences in the mode of parasitism and life forms of the study species. For instance, *P. lanceolata* and *C. maritimus* subsp. *maritimus* are both root hemiparasites that do not climb other vegetation, whereas *C. pubescens* parasitizes shoots and is a climbing vine.

Pedicularis lanceolata performed worse in the greenhouse with clipped hosts than with unclipped hosts regardless of host type (Fig. 2.1). I note, however, that the densities in this experiment (three plants per pot) were relatively low and that if higher densities of host plants were used in this study there may have been a stronger effect of aboveground competition on *P. lanceolata* growth by the different host plant types. Such strong effects have been found for plants when either competitive (Tilman 1982) or facilitative (Chu *et al.* 2009) interactions predominate.

Survivorship, growth, haustorial production, and reproduction of *P. lanceolata* grown in the greenhouse with mixed native and invasive hosts was intermediate between these responses when it was grown with only native or only invasive hosts. This result, along with the consistency of these trends in the clipped replicates, suggests that the mere presence of the two invasive species used in this study negatively affected *P. lanceolata* through some mechanism other than above-ground competition for light. Fellows and Zedler (2005) proposed a possible "pseudo-host" effect in which there is an energetic cost for the hemiparasite of making poorly-functional haustoria with non-native invasive hosts. Confirmation of the functionality of haustorial connections is possible by tracing the flow of secondary compounds from host to hemiparasite or by microscopically inspecting the anatomy of the haustorial connection for penetration of the host root (Marvier & Smith 1998, Calladine *et al.* 2000), but such assays were beyond the scope of this study.

A limitation of any greenhouse study is that conditions within a greenhouse are not identical to field conditions. For instance, many more than four species interact with *P. lanceolata* in the field. In the field removal experiment, the response of *P. lanceolata*

growth and survival to the removal of non-natives was variable from year to year. In the first year of the study, *P. lanceolata* growth was greater in two of the three plots where non-natives were removed compared to the growth of *P. lanceolata* in plots with the other three treatments. However, in the second year of the study, the largest increase in growth from 2008 to 2009 was in a plot where natives were removed. During the course of the study, a native shrub, *Alnus incana* ssp. *rugosa* (Du Roi) Clausen, became more dominant at the site where the removal plots were located. This transition of the site from an early successional to a mid-successional habitat as a result of the growth of a native shrub might explain the variable effects of the native and non-native removal treatments over the course of the study. In a demographic study at the same site as the removal experiment, uninvaded patches had higher population growth rates in 2007-2008, but in 2008-2009 uninvaded patches had lower growth rates than invaded patches. This difference in the population growth rates over the two years of the study also was likely due to succession of native shrubs.

This result stresses the importance of complementing greenhouse studies with field studies. Other studies also have found that greenhouse dynamics may not account for all of the variables that occur in the field. For instance, in a study of host preference of the rare root hemiparasite *Castilleja levisecta* Greenm., Lawrence and Kaye (2008) found significant indirect effects of vole herbivory associated with different host plants in the field but not in the greenhouse where voles were absent.

The combination of greenhouse and field studies also stresses the importance of considering multiple threats to rare species, as both invasive species and succession have negative effects on *P. lanceolata*. The results presented here suggest that the removal

either of co-occurring invasive *B. inermis* and *P. arundinacea* or of native woody vegetation may benefit *P. lanceolata*, but eradication and restoration methods would need to be well planned. For instance, the use of systemic herbicides to control invasive species could inadvertently translocate herbicides to the hemiparasite. Selective clipping of invasive species is a possible solution, but careful removal of only invasive species is crucial. The results of the greenhouse study clearly illustrate that clipping of some hosts reduces *P. lanceolata* biomass and decreases flower production. In the removal experiment, *P. lanceolata* growing in plots where all surrounding plants were removed had high mortality and low growth. Selective clipping treatments, however, are labor intensive and require individuals trained in plant identification skills. In heavily invaded areas where invasive species may be the only host plants in the vicinity of the hemiparasite, immediate restoration of native host plants also would be necessary. As with many invasive species removal scenarios, the best management may be to prevent the invasion in the first place.

There are accounts of both successful and unintentionally disastrous removals of invasive species in attempts to benefit native biota and ecosystem processes (Bergstrom 2009, Simberloff 2009). Organisms with unique ecologies that benefit from facilitative interactions with other species, such as hemiparasitic plants, may be more susceptible to unintentional negative effects of invasive species eradications. Much of the literature on invasive species focuses on competitive exclusion of native species by invasive species, and there are few documented examples of instances where invasive species disrupt existing associations between native species (*e.g.*, Stinson *et al.* 2006). These results

presented here highlight the importance of considering facilitations and multiple threats, including impacts from certain native species, when determining the impacts of invasive species on native species.

Table 2.1. Host species arrays for the three levels of host type. Each replicate (pot) contained an individual *P. lanceolata* with two host plants.

Native	Mixed native and invasive	Invasive
J. effusus : J. effusus	*J. effusus : B. inermis*	*B. inermis : B. inermis*
S. cyperinus : S. cyperinus	*J. effusus : P. arundinacea*	*P. arundinacea : P. arundinacea*
	S. cyperinus : B. inermis	*B. inermis : P. arundinacea*
	S. cyperinus : P. arundinacea	

Table 2.2. Results of generalized linear models testing the responses of *P. lanceolata* survival from fall 2008 to spring 2009, *P. lanceolata* total biomass, the total number of haustoria per pot, and the number of inflorescences produced by *P. lanceolata* at the time of the second harvest to all or a subset of the following effects: clipping treatment (treatment), host type, *P. lanceolata* source population (source), *P. lanceolata* initial size (initial size), *P. lanceolata* transplant date (transplant date), total host biomass, harvest and a clipping treatment × host type interaction. Corresponding error distributions used for the separate models are in parentheses below the response variable. A * denotes *P*-values with significant effects where $\alpha = 0.05$.

Response (Error distribution)	Effect	*df*	M.S.	*F*	*P*
P. lanceolata survival (Binomial)	Treatment	1	0.113	0.566	0.453
	Host type	2	1.46	7.33	<0.001*
	Source	1	0.142	0.710	0.400
	Initial size	1	0.818	4.10	0.0439*
	Transplant date	2	0.330	1.65	0.199
	Treatment × host type	2	0.298	1.50	0.226
	Residual	232	0.199		
P. lanceolata biomass (Gaussian)	Treatment	1	18.6	13.3	<0.001*
	Host type	2	57.0	40.8	<0.001*
	Source	1	5.40	3.87	0.0510
	Initial size	1	1.04	0.746	0.389
	Transplant date	1	4.50	3.22	0.0747
	Harvest	1	2.40	1.72	0.192
	Total host biomass	1	3.35	2.40	0.124
	Treatment × host type	2	2.06	1.48	0.231
	Residual	151	1.40		
# of haustoria per pot (Poisson)	Treatment	1	9522806	31.4	<0.001*
	Host type	2	2627580	6.68	<0.001*
	Source	1	2619732	8.65	0.00378*
	Initial size	1	3272	0.0108	0.917
	Transplant date	1	885788	2.93	0.0892
	Harvest	1	31532	0.104	0.747
	Total host biomass	1	3427004	11.3	<0.001*
	Treatment × host type	2	448661	1.48	0.231
	Residual	151	302818		

Continued on next page

Table 2.2, continued					
# of inflorescences (Poisson)	Treatment	1	26.3	10.2	0.00202*
	Host type	2	42.7	16.6	<0.001*
	Source	1	0.071	0.278	0.868
	Initial size	1	1.16	0.451	0.504
	Transplant date	1	4.09	1.59	0.211
	Total host biomass	1	0.522	0.203	0.653
	Treatment × host type	2	8.63	3.36	0.040*
	Residual	74	2.57		

Table 2.3. Names and origins (native or non-native) of species growing in the field removal experimental plots. Non-native species with a "*" have both non-native and native genotypes, but were considered non-native in the removal treatments (USDA 2009). Nomenclature follows the Integrated Taxonomic Information System (Integrated Taxonomic Information System 2010).

Species	Origin
Acer rubrum L.	Native
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Native
Ambrosia artemisifolia L.	Native
Amphicarpea bracteata (L.) Fern.	Native
Aclepias incarnate L.	Native
Bidens vulgate Greene	Native
Boehmeria cylindrical (L.) Sw.	Native
Bromus inermis Leyss.	Non-native
Cicuta maculata L.	Native
Daucus carota L.	Non-native
Fragaria virginiana Duchesne	Native
Frangula alnus P. Mill.	Non-native
Gentiana linearis Froel.	Native
Hypericum mutilum L.	Native
Impatiens capensis Meerb.	Native
Juncus effusus L.	Native
Lonicera morrowii Gray	Non-native
Lycopus americanus Muhl. ex. W. Bart.	Native

Continued on next page

Table 2.3, continued

Lycopus uniflorus Michx.	Native
Lysimachia ciliata L.	Native
Oxalis stricta L.	Native
Phalaris arundinacea L.	Non-native*
Plantago major L.	Non-native
Poa pretense L.	Non-native*
Polygonum sagittatum L.	Native
Potentilla simplex Michx.	Native
Rumex acetosella L.	Non-native
Solidago gigantean Ait.	Native
Solidago rugosa P. Mill.	Native
Solidago uliginosa Nutt.	Native
Symphyotrichum lanceolatium var. *lanceolatum* (Willd.) Nesom	Native
Taraxacum officinale F.H. Wigg.	Non-native*
Toxicodendron radicans (L.) Kuntze	Native
Trifolium incarnatum L.	Non-native

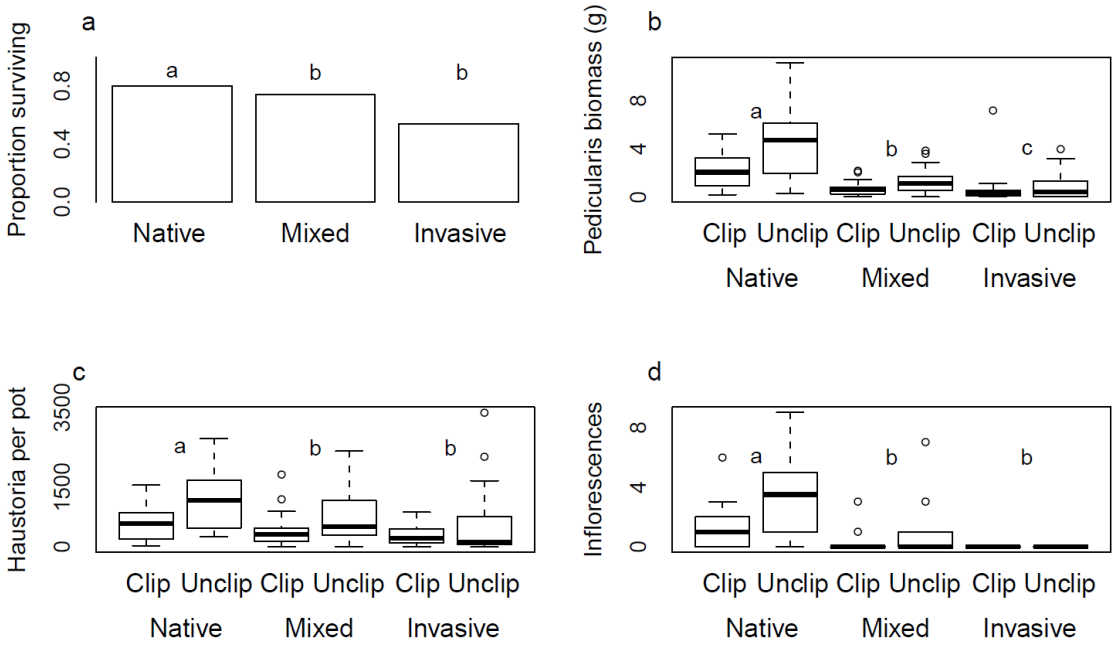

Figure 2.1. Responses of *P. lanceolata* (a) over winter survival, (b) total biomass, (c) number of haustoria produced per pot, and (d) number of inflorescences to host type (natives only, mixed native and invasive, and invasives only) and/or clipping treatment. Host types not sharing a lower case letter were significantly different according to Tukey's Honest Significant Differences test.

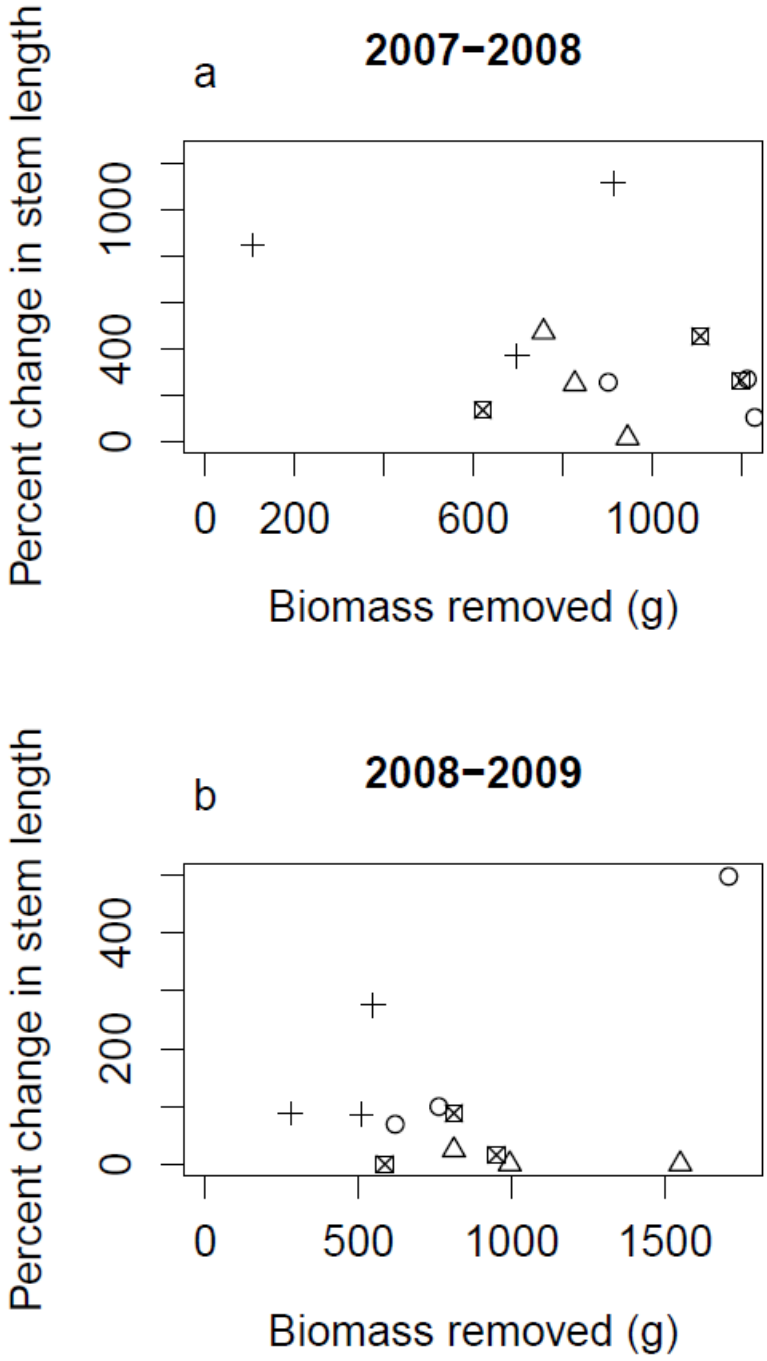

Figure 2.2. Percent change in stem length of *P. lanceolata* and corresponding amount of biomass removed in the removal plots in (a) 2007-2008 and (b) 2008-2009. The symbols for the treatments are: open circles (natives removed), crosses (non-natives removed), squares with an 'x' (controls), and open triangles (both native and non-natives removed).

CHAPTER III

INVESTIGATING THE IMPACT OF INVASIVE SPECIES ON THE POPULATION DYNAMICS OF A RARE NATIVE PERENNIAL WITH INTEGRAL PROJECTION MODELS

Abstract

Although invasive species are considered to be the second greatest threat to rare native species, few studies rigorously quantify detrimental effects by invasive species on the persistence of rare species. Demographic modeling provides a useful tool for determining the effects of invasive species on population growth rates of rare species, but estimates from traditional matrix models may have high levels of uncertainty when data are sparse, as is common when dealing with rare species. In this study, I use Integral Projection Models, which have been shown to produce lower variance and bias in estimates of population growth, to compare the population dynamics of a regionally rare perennial, *Pedicularis lanceolata*, growing in uninvaded and invaded patches. In stochastic simulations, the population growth rate (λ) was lower in uninvaded patches than in invaded patches. When temporal variation was deterministic, the population growth rate was greater for uninvaded patches in 2007-2008, but was greater for invaded patches in 2008-2009. Sensitivity and elasticity analyses showed that in uninvaded and invaded patches, seed production, growth, and recruit size had the most influence on λ in both years of the study. A life table response experiment found that decreased survival, flowering, and seed production in 2007-2008, and decreased seed production in 2008-2009, contributed most to the observed difference in λ between invaded and uninvaded patches. A transition to mid-successional habitat from the early successional habitat

preferred by *P. lanceolata* may explain the lower population growth rates observed in 2008-2009 in uninvaded patches. Invasive species may be just one of many drivers of the population dynamics of the rare species of interest and this study highlights the importance of considering multiple threats when managing for the persistence of rare native species.

Introduction

A review of approximately 2,500 imperiled or federally listed species in the United States found that competition with, or predation by, invasive, non-native species (hereafter referred to as "invasives") was the second greatest threat to imperiled species after habitat destruction, affecting 49% of the analyzed species (Wilcove *et al.* 2000). There are a number of studies that assess the effects of additions or removals of invasive species on different vital rates of rare plants (*e.g*, Harrod and Halpern 2005, Miller and Duncan 2004, Huenneke and Thomson 2005). However, to understand how invasive species influence the persistence of populations of rare species over time periods greater than the length of most addition or removal experiments, it can be useful to incorporate demographic modeling into answering questions about the effects of invasive species on rare plants (Thomson 2005).

Demographic matrix models are one of the most commonly used tools for modeling population dynamics (Caswell 2001), but without long-term data sets, uncertainty in the estimates of demographic matrix models may be considerable (Doak *et al.* 2005, Ellner and Fieberg 2003). Integral Projection Models (IPMs) are one alternative to matrix models. Unlike stage-based demographic matrix models that separate individuals within a population into discrete categories, IPMs treat structuring variables

such as size and age as continuous (Easterling *et al.* 2000). The treatment of age and size as continuous variables in the IPM framework is compelling because fewer parameters need to be estimated and variables that are continuous do not need to be forced into discrete categories (Ellner and Rees 2006). In fact, IPMs generally result in estimates of population growth rates (λ) with lower bias and variance than the estimates of matrix models for two perennial herbs (Ramula *et al.* 2009).

In this paper, I use Bayesian IPMs to determine the effects of invasive species on the persistence of a regionally rare hemiparasitic plant species, swamp lousewort (*Pedicularis lanceolata* Michx.). Although *P. lanceolata* is globally secure (conservation rank "G5", sensu NatureServe (2009)), many New England states consider the species to be of regional conservation concern and there is only one extant population of *P. lanceolata* in the entire state of Massachusetts (Brumback *et al.* 1996, NatureServe 2010). In New England, threats to *P. lanceolata* include invasive species, competition with woody vegetation as a result of habitat succession, being run over by all-terrain vehicles, and changes in hydrologic regimes (Allard 2001, Farnsworth *et al.* 2007). Invasive species occur frequently with *P. lanceolata* throughout its geographic range (Chapter I). Because a greenhouse experiment showed that *P. lanceolata* had higher rates of growth, survival, and flowering when growing with native graminoids than when growing with invasive grasses (Chapter II), it is reasonable to hypothesize that invasive species would have a negative impact on the population growth rate of this species.

Here, I address three questions about the persistence of *P. lanceolata* growing in uninvaded and invaded patches to better understand the interaction between this rare plant and the invasive species with which it grows. First, are the population growth rates

of *P. lanceolata* different in uninvaded and invaded patches? If *P. lanceolata*'s vital rates are more variable from year to year when it grows with invasive plants, then the population's persistence may be affected more negatively by the presence of invasives (Williams and Crone 2006). To incorporate this variation, I calculated the population growth rate using models that treat temporal variation as stochastic. Second, if there are differences in the population growth rates between uninvaded and invaded patches, which vital rates are most influenced by the presence of invasive species? Third, which vital rates contribute most to differences in the population growth rates in uninvaded and invaded patches? The methods and models are general and provide a framework for assessing the impact of invasive species on the demography of native species, both rare and common.

Methods

Study system

Pedicularis lanceolata is a rare short-lived, non-clonal perennial plant (Allard 2001). Its geographic range extends from the Midwest of North America to its eastern coast with populations as far south as Georgia and as far north as the Canadian provinces of Manitoba and Quebec (NatureServe 2010). Documented habitats of *P. lanceolata* include sunny, early successional areas that experience periodic flooding, such as wet meadows, fens, and stream-sides (Piehl 1965, Farnsworth *et al.* 2007). Seeds of *P. lanceolata* germinate and produce seedlings in mid- to late spring. Flowering occurs late in the summer, and visitation by bumblebees (*Bombus* spp.) ensures pollination of the obligately out-crossed flowers (Macior 1969). As a generalist hemiparasite, *P. lanceolata*

requires supplemental nutrients from a host plant in order to complete its life cycle (Lackney 1981). Both natives and invasives can serve as hosts for *P. lanceolata*, but it grows better when growing with native hosts (Chapter II).

Field methods

I collected demographic data on a population of *P. lanceolata* in western Massachusetts from 2007 to 2009. The invasive grasses reed canary grass (*Phalaris arundinacea* L.) and smooth brome (*Bromus inermis* Leyss.) were abundant at the site. There are both native and non-native genotypes of *P. arundinacea* in North America, but the *P. arundinacea* growing with the Massachusetts population of *P. lanceolata* was considered to be invasive because this species was likely planted into the area to supply fodder when cattle were pastured from the 1840s to the 1980s along the stream where *P. lanceolata* grows (Appendix I). Many of the non-native genotypes of *P. arundinacea* were imported to North America from Asia to provide fodder for cattle (Morrison and Molofsky 1999). Other invasive species at the site included glossy buckthorn (*Frangula alnus* P. Mill.), Morrow's honeysuckle (*Lonicera morrowii* A. Gray), and multiflora rose (*Rosa multiflora* Thunb.). The most abundant native species were alders (*Alnus* spp.), common boneset (*Eupatorium perfoliatum* L.), shallow sedge (*Carex lurida* Wahlenb.), tall goldenrod (*Solidago gigantea* Aiton), and wrinkleleaf goldenrod (*Solidago rugosa* Mill.).

In 2007, I established a 0.1-ha monitoring area that represented ~80% of the known *P. lanceolata* population in the area, which I divided up into 1 × 1 m grid cells. Each year I recorded the percent cover class of invasive species in each grid cell. There were five cover classes corresponding to the percent cover of invasive species per grid

cell: 0%, 1-5%, 6-25%, 26-50%, 51-75%, and 76-100%. To parameterize the model, I selected grid cells that were in the centers of uninvaded or invaded patches and several meters from the edge of a patch to avoid shading of, or host use by, *P. lanceolata* from plants in neighboring grid cells. Selecting grid cells in the center of invaded or uninvaded patches also ensured that the invasion status of a grid cell in the model did not change noticeably over the course of the study. There were 48 selected grid cells in invaded patches and 47 selected grid cells in uninvaded patches. To confirm that the presence or absence of invasive species was not driven by abiotic factors, I measured the slope in the center of each selected grid cell and performed a logistic regression analysis where slope was the predictor and the presence or absence of invasive species was the response. I also recorded the aspect in the center of each selected grid cell and whether each cell was covered in water or not during winter and spring floods in 2008 and 2009 to determine whether the presence or absence of invasive species was driven by hydrology or aspect in a contingency table analysis.

Within each selected grid cell, I marked all *P. lanceolata* individuals with aluminum tags and recorded their locations. In 2007, 2008, and 2009, I recorded the presence of and tagged any new seedlings, in late May. In late August of each year, I relocated the tags and recorded survival, the total number of leaves of all stems, the length of all stems, and whether or not each plant was flowering. In late September of each year I recorded the total number of seed capsules produced by each flowering plant. Finally, in October of each year I collected all of the flowering capsules from fifteen randomly selected plants (eight plants in invaded patches and seven in uninvaded

patches) to quantify seed set and seed herbivory. Ideally, seed set would have been quantified on plants from each grid cell, but the permits for working with this rare species only allowed for the sampling of fifteen plants.

Model structure

An IPM uses the following equation to project population dynamics from time *t* to time *t*+1:

$$n(y) = \int_{\Omega} k(y,x)n(x)\mathrm{d}x \qquad (1)$$

where *x* is an individual's size at time *t*, *y* is an individual's size at time *t*+1, and Ω is the range of possible sizes for individuals within the population. An IPM employs a distribution function $n(x)$ in place of the population vector of traditional matrix models. The derivative of this distribution function is the number of individuals whose size falls within the range of $[x, x + \mathrm{d}x]$. In an IPM, the projection kernel $k(y,x)$ is equivalent to the transition matrix **A** in a matrix model and multiplication of the distribution function $n(x)$ by the kernel $k(y, x)$ gives the number of individuals of size *x* at time *t* that survive and are size *y* at time *t*+1.

Two functions describing survival and growth $p(x, y)$ and fecundity $f(x, y)$ make up the kernel (Ellner and Rees 2006):

$$n(y) = \int_{\Omega} [p(x,y)f(x,y)]n(x)\mathrm{d}x \qquad (2).$$

The survival and growth function is $p(x, y) = p_s(x)\, g(x, y)$ where $p_s(x)$ is the probability that an individual of size *x* survives until time *t*+1, and $g(x, y)$ describes the growth of an individual of size *x* to size *y* during the time step. The fecundity function is $f(x, y) = p_f(x)\, f_n(x)\, f_d(y)\, p_e$ where $p_f(x)$ is the probability that a plant of size *x* flowers, $f_n(x)$ is the number of seeds produced by an individual of size *x*, $f_d(y)$ is the size distribution of

recruits in time t+1, and p_e is the probability of establishment for a seedling (Williams and Crone 2006). The various probabilities that make up the survival-growth or fecundity kernels are estimated by fitting continuous functions to the data (*e.g.*, regressions). Similar to other studies that model demographics with IPMs (*e.g*, Rose *et al.* 2005, Williams and Crone 2006), the model presented in this paper assumes that there is no correlation between seedling and parent sizes.

Testing for temporal variation

If the vital rates of a rare native plant are more variable when it is growing with invasives (Williams and Crone 2006), then the presence of the invasive species may more negatively affect the population growth rate of *P. lanceolata*. To determine whether or not temporal variation might impact the model, I tested for main and interactive year effects for all of the models used to estimate the vital rates (Fig. 3.1). I used maximum-likelihood equivalents of these models because it is not possible to calculate Bayes Factors to determine statistical significance of terms in models such as logistic regressions where weakly informative priors are not conjugate (Marin and Robert 2007, Gelman *et al.* 2008). Year effects were significant for all of the models in Figure 3.1 (see Results).

A modeler can treat temporal variation in an IPM as deterministic or stochastic (Ellner and Rees 2006, Rees and Ellner 2009). When temporal variation in an IPM is deterministic, a modeler estimates the probabilities that make up the survival-growth and fecundity kernels for a single year of data using fixed effects models (Fig. 3.1). From these estimates a single projection kernel is constructed, and calculations of the population growth rate (λ) or forecasts of population size are then based on this single

projection kernel (Ellner and Rees 2006). There are two ways of including stochastic temporal variation in an IPM. One is to estimate fixed effects models for each year of data separately, then to estimate a projection kernel for each year of data and randomly select from the set of year-specific projection kernels to calculate an average stochastic λ or to forecast population size (Childs *et al.* 2004). This first method of incorporating stochastic temporal variation into an IPM is equivalent to matrix selection in demographic matrix models (Ellner and Rees 2009). A second approach to incorporating stochastic temporal variation is to fit mixed-effects models to estimate the probabilities from which the survival-growth and fecundity kernels are comprised (Rees and Ellner 2009, Table 3.1). In these mixed-effects models, to calculate an average stochastic λ or project population size, each year random effects are drawn from probability distributions for certain parameters (Pinheiro and Bates 2000). This second approach to stochastic temporal variation is similar to element selection in demographic matrix models. Ellner and Rees (2009) recommend fitting stochastic models with temporal variation treated as a "fixed" effect when there are only a few years of data because such limited data may not contain enough information to provide reliable probability distributions for the random factors in a mixed-effects model. Further, in a recent paper Bolker *et al.* (2009) describe issues that statisticians have in estimating the parameters for mixed-effects models and outline instances where procedures in standard statistical software used by many ecologists (*e.g*, SAS and R) may provide spurious *P* values. Given these issues with mixed-effects models, and since the data for this study only spanned a few years, I treated stochastic temporal variation as a fixed effect.

Estimation of vital rates

All demographic parameters were estimated within a Bayesian framework because the estimated Bayesian posterior distributions, as opposed to point estimates in maximum likelihood models, made it straightforward to incorporate estimation error into subsequent population projections, sensitivity analyses, and life table response experiments. Size was modeled as the *ln* (total number of leaves per plant +1) for all models of vital rates. The range of sizes that the continuous functions of the IPM spanned were set to the observed sizes of plants in the field study.

For the survival-growth kernel, the probability of survival was modeled by a Bayesian logistic regression with size *x* as the predictor variable (see Fig. 3.1 for details on priors). I analyzed individual growth with Bayesian linear models where size *y* was a function of size *x* (Fig. 3.1). For the fecundity kernel, I estimated flowering probability with a Bayesian logistic regression model and seed production with a Bayesian Poisson regression where size *x* was the predictor for both models (Fig. 3.1). Data on the seed bank dynamics of *P. lanceolata* were lacking, so I set the probability of establishment equal to the total number of recruits per patch type divided by the number of seeds produced per patch type (Ellner and Rees 2006). A normal distribution truncated at zero described the size distribution of recruits well (Figs. 3.2e-3.5e), so I modeled the distribution of recruit sizes with a Bayesian normal distribution.

I performed all analyses with the MCMCpack and Stats packages of R statistical software (R Development Core Team 2010). I confirmed that all estimated posterior distributions converged by verifying that the acceptance rates of all Markov Chain Monte Carlo simulations were between 0.2 and 0.5 and by examining trace plots of the sampled

parameter values versus the iteration number for all models to confirm that the parameters reached stationary distributions (Marin and Robert 2007). Code for the analyses is in Appendix B.

This model did not include does not include density dependence or seed bank dynamics. In other IPMs (*e.g.*, Ellner and Rees 2006), density dependence was incorporated into the model by using a modified parameter for recruitment (*i.e.*, the probability of establishment). In this study, whether or not recruitment depended on density was irrelevant to my goal, since I was interested in making comparisons between uninvaded and invaded patches of the measured recruitment at the observed densities of *P. lanceolata*. Seed bank dynamics were not included in the model because data on the seed bank of *P. lanceolata* were lacking. However, with detailed information on seed germination and mortality an additional parameter for the seed bank could be included in future versions of this model.

Population growth estimates, sensitivity analyses, and life table response experiment

During each iteration of an IPM, the integrals of the kernel are calculated numerically with an approximating matrix (Easterling *et al.* 2000). The number of size categories (*i.e.*, mesh points) in the approximating matrix was determined by selecting the smallest matrix that produced similar values of the population growth rate (λ) compared with larger matrices (Ellner & Rees 2006, Fig. 3.6). Iterating the IPM until convergence on the solution to the complex integral of the kernel yields an approximating matrix whose dominant eigenvalue is the population growth rate (λ) and dominant eigenvector is the stable state distribution (w). The dominant left eigenvector of the

transpose of the approximating matrix is the state dependent reproductive value (v) (Ellner and Rees 2006). With values for λ, w, and v it is possible to carry out simulations of population growth rate, sensitivity analyses, and life table response experiments.

I estimated the population growth rate (λ) with temporal variation treated as either deterministic or stochastic using fixed effects models (Table 3.1). For the deterministic model, I sampled from the posteriors of the vital rates for a single year (*e.g.*, 2007-2008 or 2008-2009). For the stochastic model, at each time step I randomly selected from the 2007-2008 or 2008-2009 vital rate estimates to incorporate yearly variation (Childs *et al.* 2003). I ran each deterministic and stochastic model 1000 times sampling from the posterior distributions of the coefficients for the vital rates to incorporate estimation error into estimates of the population growth rate.

I conducted sensitivity and elasticity analyses to determine how absolute and proportional changes, respectively, in the vital rates affect *P. lanceolata* persistence in uninvaded and invaded patches (Caswell 1978). Sensitivity analysis quantifies changes in λ resulting from relatively small changes in particular vital rates when all other values are kept constant (Morris and Doak 2002). I manually perturbed coefficients by adding 0.05 to the vital rate of interest. Perturbations of 0.01 and 0.10 yielded similar results. The sensitivity was then calculated as the observed change in λ from the perturbation divided by the perturbation size (Caswell 1978). To account for estimation error in sensitivity estimates, I held all but one demographic parameter (*e.g*, the slope coefficient for the logistic regression of fecundity) constant and sampled from its posterior distribution 1000 times (Ackakaya and Sjögren-Gulve 2000) then took the average and standard deviation of the distribution of sensitivities. This procedure was repeated for each demographic

parameter in turn. To calculate elasticities, I multiplied the sensitivity by the ratio of the mean estimate for the coefficient and the mean estimate of λ (Caswell *et al.* 1984, de Kroon *et al.* 1986). I separately summed the sensitivities and elasticities of demographic parameters for each vital rate to scale up from calculations of sensitivities and elasticities of demographic parameters to those of vital rates.

I conducted a life table response experiment where the uninvaded patches were the "controls" and the invaded patches were the "treatments" to separate out the effects of patch type (uninvaded or invaded) on the contributions of each vital rate's influence on the deterministic population growth rate (λ) (Caswell 2001). For all vital rates except for recruit size, the LTRE analysis followed the approach of Thomson (2006) where the contribution of each vital rate was the difference between the parameter value for the treatment vital rate minus the parameter value for the control vital rate multiplied by the sensitivity of the reference vital rate. The reference values came from a midpoint matrix whose elements were halfway between the parameter estimates for the treatment and the control (Caswell 2001). Unlike survival, growth, flowering, and seed production, recruit size was described by a normal distribution rather than by a linear model, so the midpoint matrix calculation was not an appropriate approach for calculating the LTRE contribution of recruit size (Williams and Crone 2006). To solve this problem, I created approximating transition matrices where recruit size was set to the value for the treatment group (invaded) and the values for all other vital rates matched the control group (uninvaded). This approach allowed me to look at changes in λ between uninvaded and invaded patches created by direct effects of recruit size.

Results

The presence or absence of invasive species did not appear to be driven by the measured abiotic factors. There was no significant effect of slope on the presence or absence of invasive species (β_0 = 0.065, $z_{2, 94 =}$ 0.180, P = 0.857; β_0 = -0.009, $z_{2, 94 =}$ -0.148, P = 0.882). There were also no significant effects of aspect or flooding on the presence or absence of invasive species ($\chi^2_{1,188}$ = 67.3, P = 0.998).

There were significant main and interactive effects of time for each vital rate (Fig. 3.1). There were especially notable year effects for survival, flowering, and seed production (Fig. 3.6). Estimates of survival were lower for small plants and higher for large plants in uninvaded patches than for similarly-sized plants in invaded patches in 2007-2008, but in 2008-2009 the probability of survival was equally high for plants in both uninvaded and invaded patches (Fig. 3.7a). Similarly, plant growth rates were lower for small plants and greater for large plants in uninvaded patches than for similarly-sized plants in invaded patches in 2007-2008 (Fig. 3.7b). These results were reversed in 2008-2009, when plant growth rates were higher for small plants and lower for large plants in uninvaded patches than in invaded patches (Fig. 3.7b). In both years, flowering probability, seed production, and seedling sizes were greater in uninvaded and invaded patches (Figs. 3.7c, d, e).

Population growth rates calculated from deterministic models showed significant differences between years ($F_{1, 3996}$ = 2.2 × 10^4, P<0.0001) and patches ($F_{2, 3996}$ = 5.6 × 10^3, P<0.0001) (Fig. 3.8). The population growth rate calculated from deterministic models in uninvaded patches was very high (λ = 6.27) in 2007-2008 and dropped in 2008-2009 (λ = 0.882). This same trend was observed for the population growth rates

calculated from deterministic models in invaded patches where $\lambda = 2.786$ in 2007-2008 and $\lambda = 1.263$ in 2008-2009. The population growth rate where temporal variation was deterministic was greater for uninvaded compared to invaded patches in 2007-2008, but this relationship between lambdas was reversed in 2008-2009 (Fig. 3.8). Population growth rates calculated from models that treated temporal variation as stochastic were greater in invaded patches than in uninvaded patches ($F_{1, 1998} = 480.55$, $P<0.0001$) (Fig. 3.8).

In both uninvaded and invaded patches during both years, sensitivities and elasticities of seed production were high, and of survival and flowering were close to zero (Fig. 3.9). Growth and recruit size had the second highest sensitivities and elasticities after seed production. Sensitivities and elasticities for growth were greater in 2008-2009, than in 2007-2008. The contributions of vital rates were variable from year to year. Survival and flowering contributed negatively in 2007-2008, but not at all in 2008-2009 to differences in the population growth rates between patches (Fig. 3.10). Growth of individual plants made no contribution to differences in λ between uninvaded and invaded patches in either year. Seed production contributed negatively to differences in the population growth rate between patches in both years. Contributions of recruit size were greater in 2008-2009 than in 2007-2008.

Discussion

Scaling up from effects of invasive species on particular vital rates of rare plants to effects of invasive species on population growth is an important step in understanding how invasive species can affect the persistence of rare native species (Thomson 2005). In both uninvaded and invaded patches, the population growth rates where temporal

variation was treated as stochastic were greater than one, and on average, λ was lower in uninvaded patches than in invaded patches. Temporal variation in λ from the stochastic models was greater in uninvaded compared to invaded patches, contrary to my initial prediction that invasives would have negative impacts on *P. lanceolata* through more variable vital rates.

The deterministic models of population growth provide additional insights into these differences in variation between patches. For both patch types, there were strong year effects. Population growth rates were greater in 2007-2008 than in 2008-2009. In 2007-2008 uninvaded patches had higher growth rates than the invaded patches, but the reverse was observed in 2008-2009. Growth of native woody vegetation, particularly alders (*Alnus* spp.), in uninvaded patches over the three years of this study is one explanation for these observed changes in the population growth rates between patches over time (Fig. 3.11). *Pedicularis lanceolata* needs ample sunlight to grow and as such often occurs in early successional habitats (*e.g*, wet meadows and open wetlands) (Allard 2001). Up until the 1980s the site had active cattle grazing, which maintained early successional habitat. With the removal of cattle from this site, the encroachment of native and invasive woody shrubs is shading out the sunny streamside habitat where *P. lanceolata* grows. The results of this study suggest that shading by native shrubs negatively impacts the population growth rate of *P. lanceolata* as much, if not slightly more, than the presence of invasive species.

Sensitivity and elasticity analyses aid in identifying critical stages in the life cycle that can be targeted for management. For *P. lanceolata*, seed production and growth had high absolute and proportional effects on the population growth rate. The effects of seed

production and growth were greater in 2008-2009 than in 2007-2008, highlighting the strong year effects in this data set. For *P. lanceolata*, survival and flowering had the lowest absolute and proportional impacts on the population growth rate.

Whether population dynamics are driven by high or low sensitivity and elasticity in vital rates is debatable (Crouse *et al.* 1987, Caswell 2000, Saether and Bakke 2000). One argument is that management should focus on components of the life cycle that have high sensitivity or elasticity, because even small changes in such traits are likely to have large impacts on population growth (Crouse *et al.* 1987). Another perspective on the management implications of sensitivity and elasticity analyses is that the parts of the life cycle with the least influence on population growth will be most responsive to environmental stress and drive population dynamics (Saether and Bakke 2000, Forbes 2010).

Although sensitivity and elasticity analyses offer insights into how much a particular vital rate influences the population growth rate, they do not provide comparisons between treatment types to identify mechanisms behind differences in treatments. The contributions of vital rates to differences in population growth rates between uninvaded and invaded patches varied from year to year. Lower survival of larger plants, flowering, and seed set contributed to lower population growth rates in invaded patches compared to uninvaded patches in 2007-2008.

In 2008-2009, seed production was the primary contributor to differences in population growth rates between patches. Unlike the previous year, the contribution of seed production in 2009 was not coupled with an equal contribution of flowering. This result may be linked to the increased shading of *P. lanceolata* in uninvaded patches in

2008-2009 due to growth of native *Alnus* shrubs. *Pedicularis lanceolata* individuals are prone to mildewing when growing in the shade, and if flowers mildew they do not set seed (SR *personal observation*). Although flowering probability was greater in uninvaded patches in both years, the percentage of mildewed plants that did not set seed was high in 2008-2009 in uninvaded patches where native cast shade (Fig. 3.11).

Despite the advantages that demographic modeling offers for answering questions about drivers of population persistence of rare species, there are limitations that will vary from model to model. A common issue with demographic models is that several years of intensive study do not produce enough data to capture the long-term population dynamics of a species (Burgman and Possingham 2000). The interaction between the effects of invasives and year on the population dynamics of *P. lanceolata* suggested by this analysis may be due to the snapshot of the invasion process and successional dynamics of the site that the sampling years captured.

The model presented in this paper was parameterized by observational rather than experimental data. While there were no obvious differences between uninvaded and invaded patches in abiotic factors such as slope, aspect, or hydrology, I cannot rule out the possibility that the results of this study may have been caused by one or more unquantified variables. In this experiment, I estimated the Bayesian posterior distributions of the vital rates using the observational data to parameterize the likelihood distribution and specified uninformative prior distributions that did not incorporate outside data. In contrast, limited amounts of data from a separate removal experiment could be incorporated into estimates of the posterior distributions for vital rates based on the observational data by specifying informed priors from the removal experiment.

Although it is not presented here, I attempted this approach using data from a separate field removal experiment on *P. lanceolata* that had small sample sizes, but the posterior distributions would not converge for most of the vital rates because the observational data forming the likelihoods of the posteriors had large variances. Although informative priors from a removal experiment were not feasible on this data set, this method may be useful for a data set that has longer term observational data, but limited data from manipulative experiments.

Demographic modeling is a key tool for understanding the factors that drive the persistence of populations of rare species (Thomson 2005). The results presented here show that invasive species may influence the persistence of *P. lanceolata*, but the temporally dependent succession of native woody shrubs also has a negative impact on the population growth rate of *P. lanceolata*. The results of this study have significant management implications for *P. lanceolata* in New England where early successional habitats have become less common in the last century (Foster and Motzkin 2003). Management efforts in New England need to consider both control of invasive species and maintenance of early successional habitat. In a review of rare species listed on the International Union of Conservation of Nature and Natural Resources (IUCN) Red List, Gurevitch and Padilla (2004) concluded that interactions with invasive species are seldom the only threat to rare native plants. This study highlights the importance of considering multiple threats to rare species in determining impacts of invasive species on the persistence of populations of rare plants.

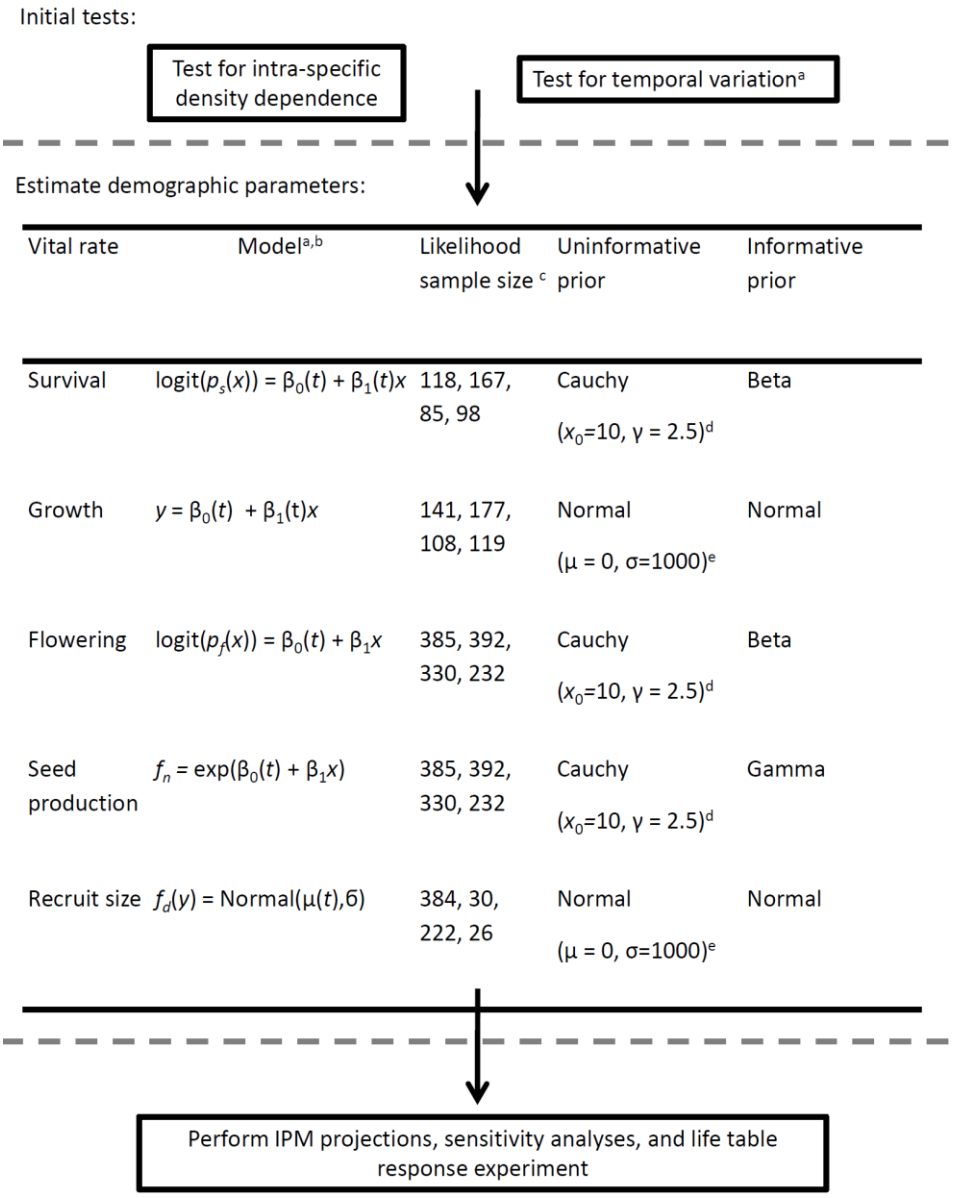

Figure 3.1. Progression of models and methods.

[a] In all instances *x* is size in year *t* measured as the *ln*(total number of leaves +1) and *y* is the size in year *t*+1.

[b] Model parameters followed by a *t* indicate significant main or interactive effects of time based on the results of the preliminary analyses to test for temporal variation.

[c] A list of sample sizes by patch type and year: uninvaded 2007-2008, uninvaded 2008-2009, invaded 2007-2008, and invaded 2008-2009.

[d] Gelman et al. 2008

[e] Marin and Robert 2007

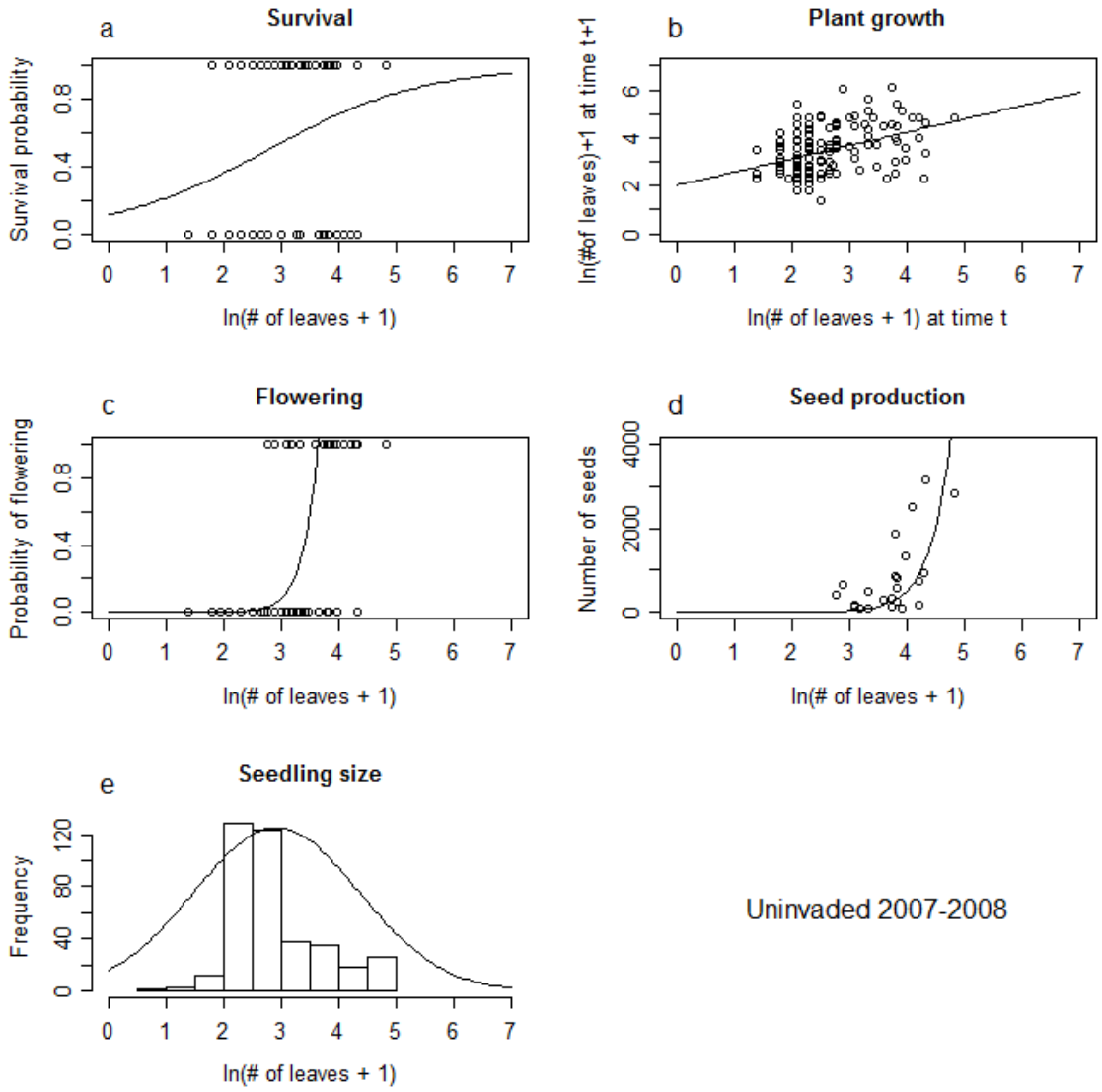

Figure 3.2. Data and estimates of the following vital rates for *P. lanceolata* growing in uninvaded patches 2007-2008: a) probability of survival, b) plant growth, c) probability of flowering, d) seed production, and e) seedling size.

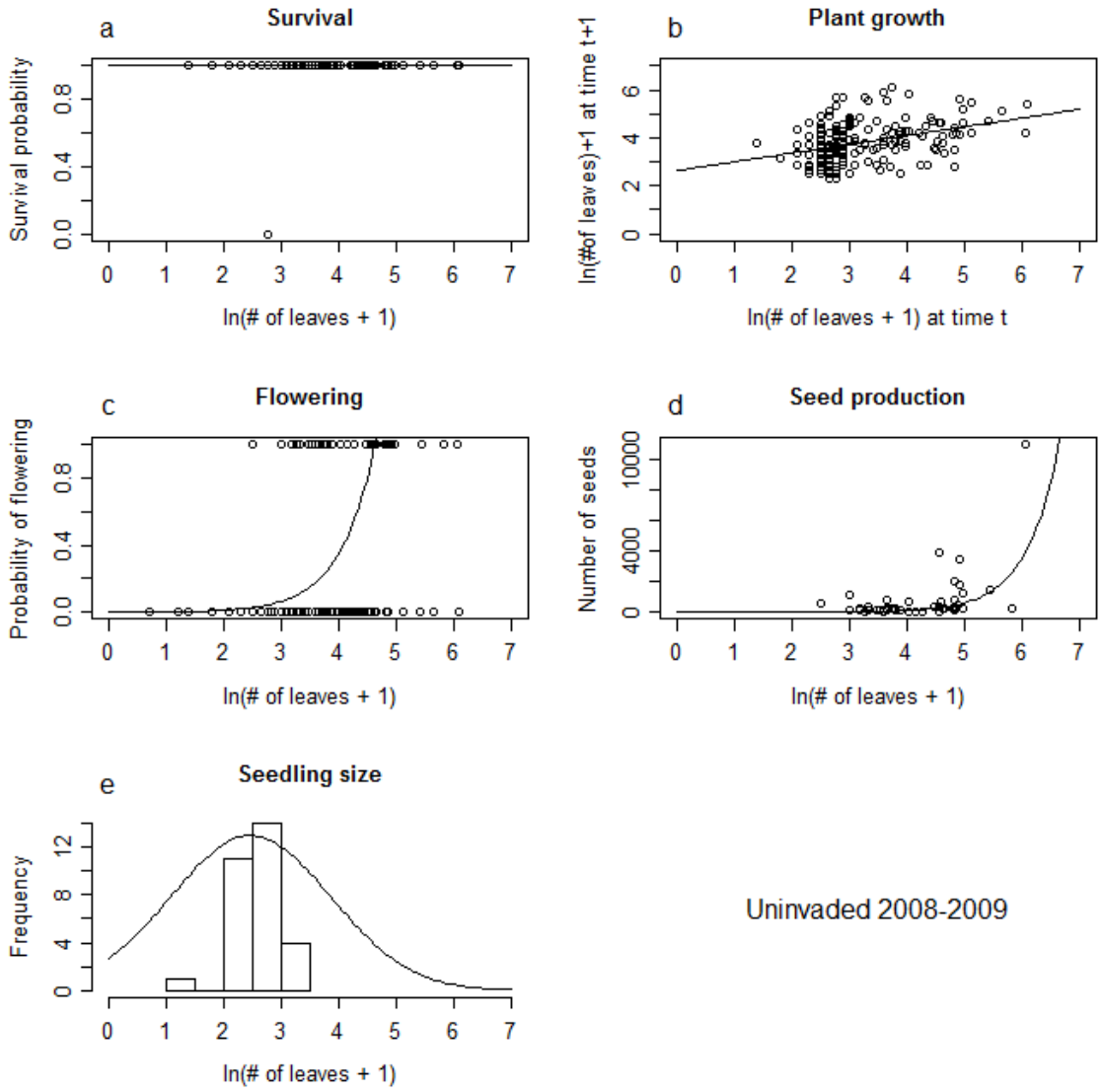

Figure 3.3. Data and estimates of the following vital rates for *P. lanceolata* growing in uninvaded patches 2008-2009: a) probability of survival, b) plant growth, c) probability of flowering, d) seed production, and e) seedling size.

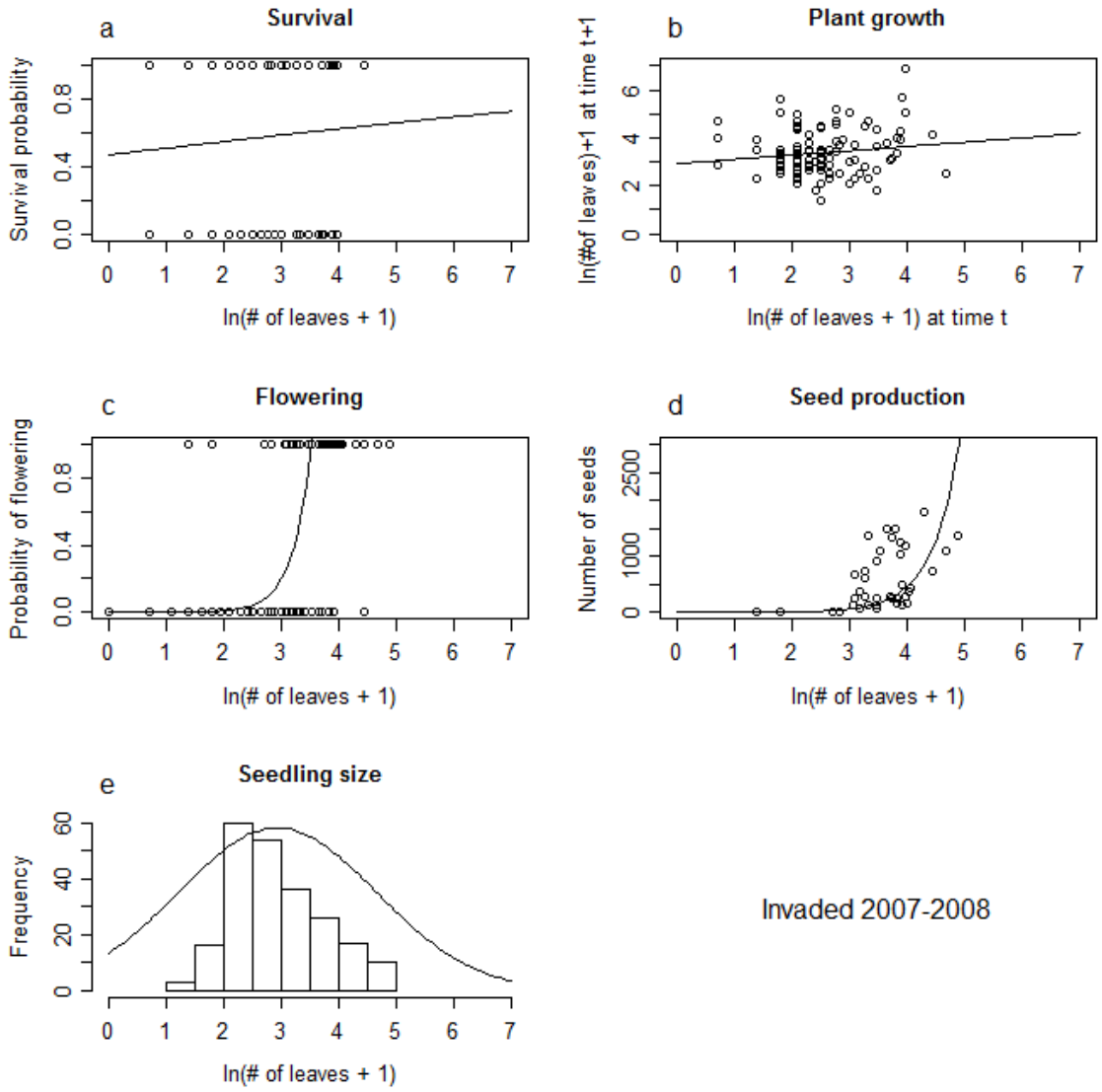

Figure 3.4. Data and estimates of the following vital rates for *P. lanceolata* growing in invaded patches 2007-2008: a) probability of survival, b) plant growth, c) probability of flowering, d) seed production, and e) seedling size.

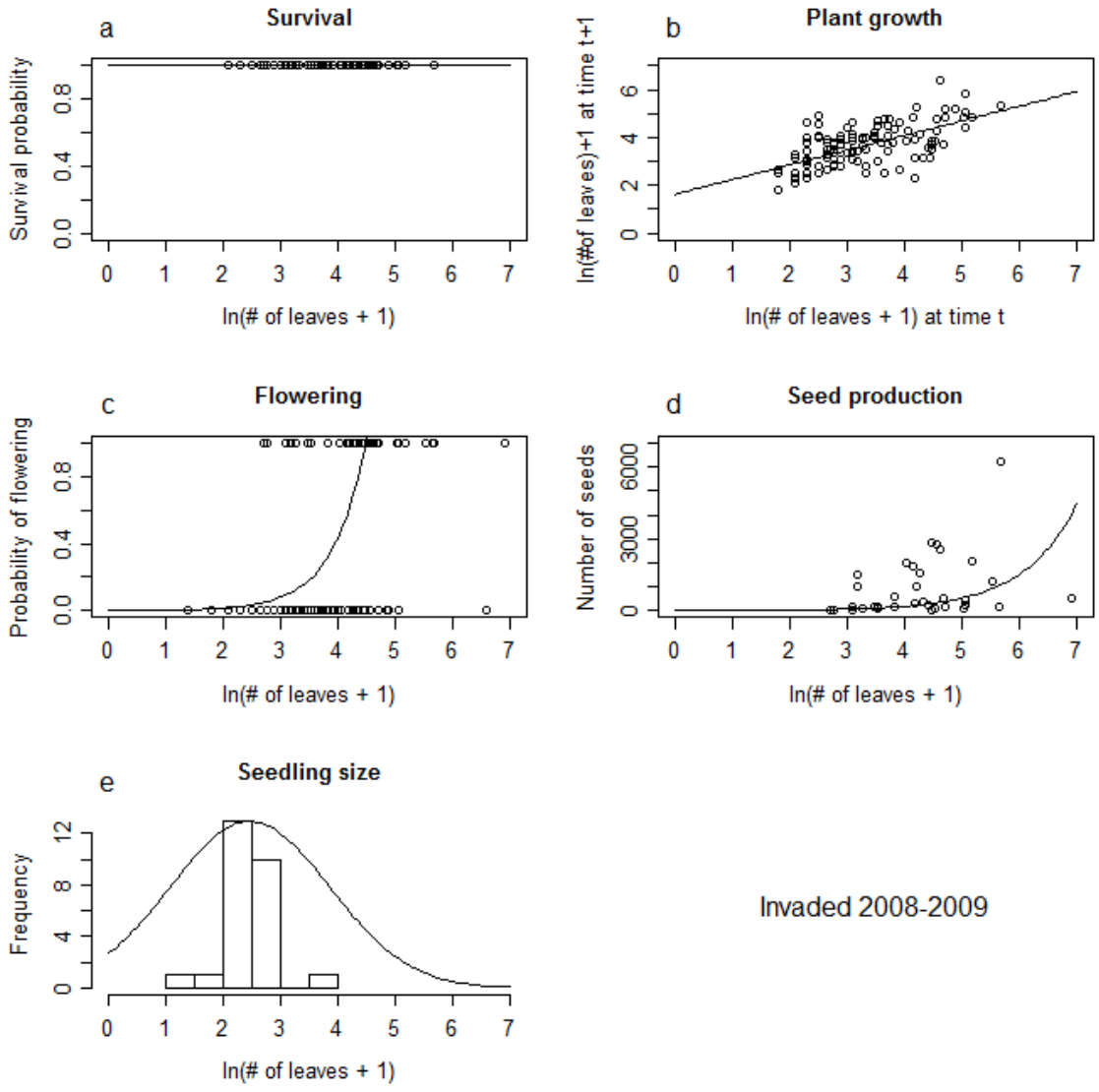

Figure 3.5. Data and estimates of the following vital rates for *P. lanceolata* growing in invaded patches 2008-2009: a) probability of survival, b) plant growth, c) probability of flowering, d) seed production, and e) seedling size.

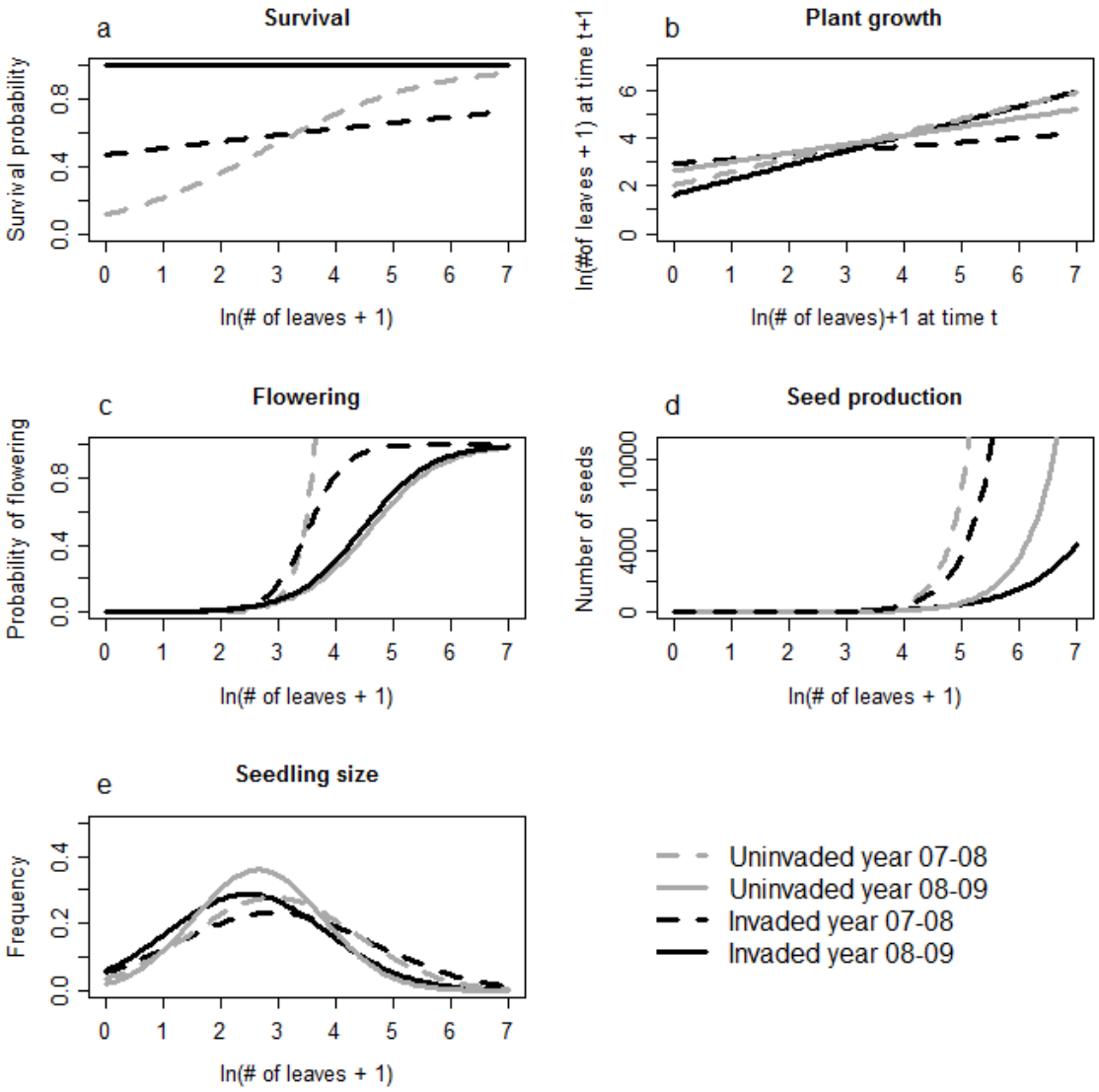

Figure 3.6. Estimates of the following vital rates for *P. lanceolata* growing in uninvaded and invaded patches during the two years of the study (2007-2008 and 2008-2009): a) probability of survival, b) plant growth, c) probability of flowering, d) seed production, and e) seedling size. Invaded and uninvaded patches in 2008-2009 both had high survival and their corresponding lines overlap in the plot.

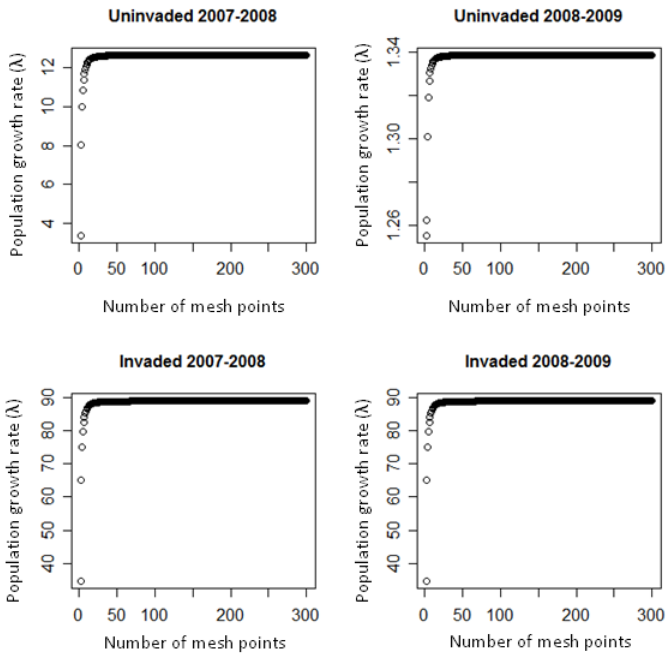

Figure 3.7. Stable estimates of the population growth rate (λ) were reached at approximately 50 mesh points for both uninvaded and invaded patches in 2007-2008 and 2008-2009. As such, approximating matrices of 100 mesh points were used for all simulations.

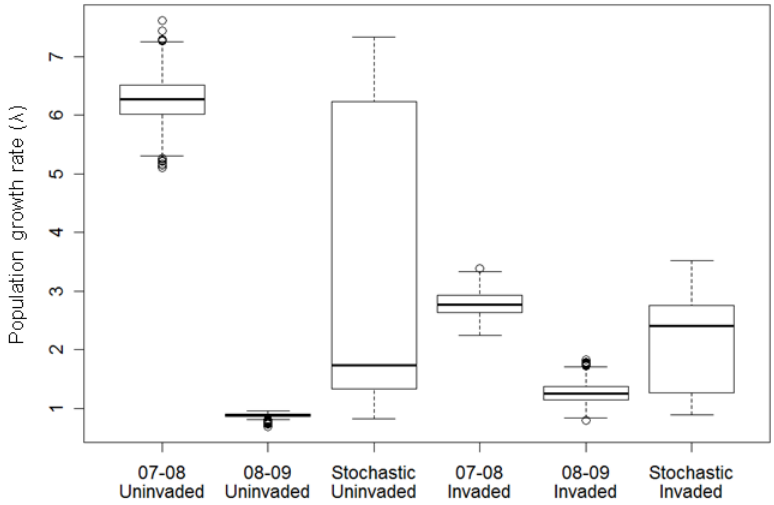

Figure 3.8. Population growth rates (λ) calculated with deterministic and stochastic temporal variation for *P. lanceolata* growing in uninvaded and invaded patches.

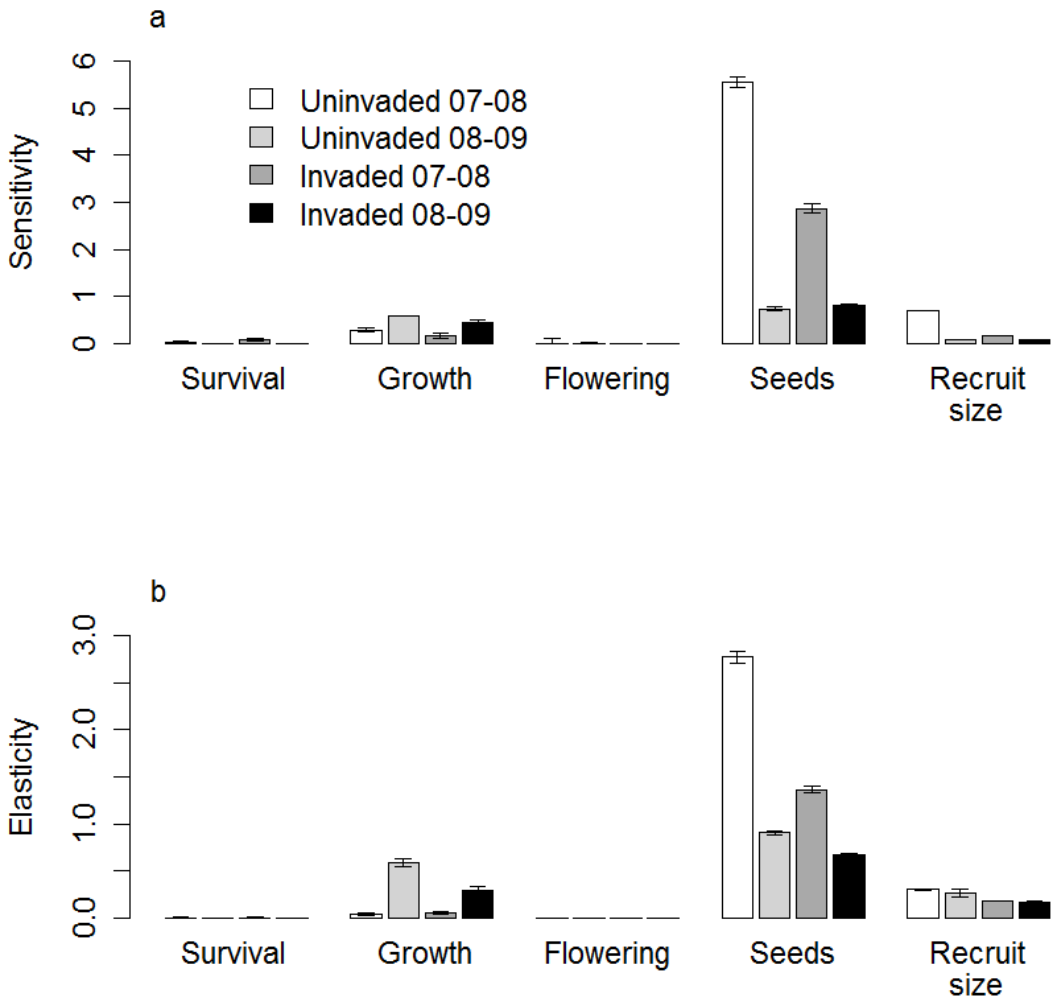

Figure 3.9. Mean (a) sensitivities and (b) elasticities of deterministic population growth rate (λ) to vital rates. Error bars indicate standard deviations. All standard deviations are plotted, but some of the sensitivities had very low standard deviations close to zero.

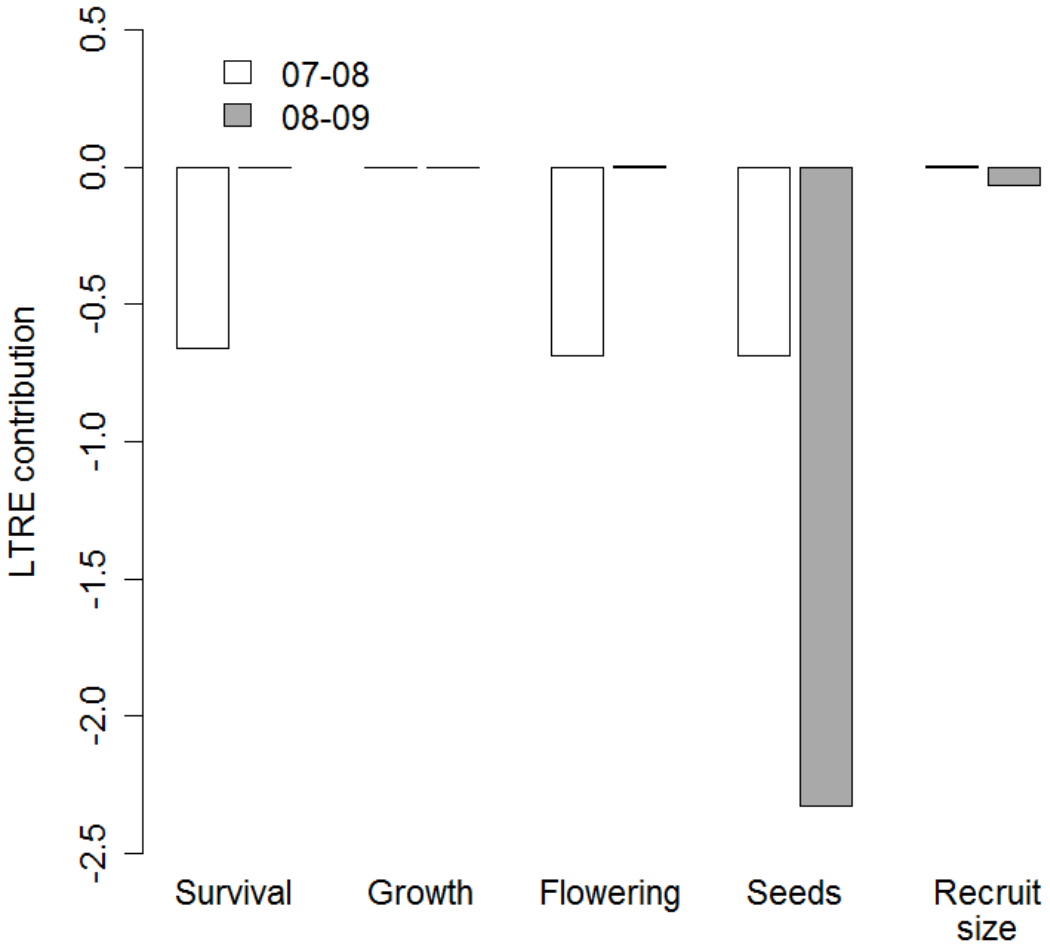

Figure 3.10. Life table response experiment (LTRE) contributions of each vital rate to changes in λ in 2007-2008 and 2008-2009. Error bars for all standard deviations are plotted, but all of the LTRE contributions had very low standard deviations close to zero.

Figure 3.11. The white arrow at the top of the photograph points to the white powdery mildew on the leaves of *P. lanceolata* growing in the shade beneath native *Alnus* species in August 2009.

CHAPTER IV

ASSESSING THE IMPACTS OF DISPERSAL, CORRELATIONS IN VITAL RATES, AND CATASTROPHIC EVENTS ON THE QUASI-EXTINCTION PROBABILITY OF A HEMIPARASITIC PERENNIAL, *PEDICULARIS LANCEOLATA*, USING AN INTEGRAL PROJECTION MODEL FOR A METAPOPULATION

Abstract

Demographic matrix models are frequently used to predict the fates of rare populations. One criticism of matrix models is that they introduce error into estimates of population growth by classifying life cycles described by continuous variables with discrete stages. Integral projection models (IPMs) avoid this issue by classifying life cycle variables as continuous ones. Despite this advantage of IPMs, there are few if any examples of applying IPMs to metapopulations. This paper develops a new, generalizable metapopulation IPM and applies it to a three year data set on a regionally rare perennial hemiparasitic plant, *Pedicularis lanceolata*. The short-term nature of the data set is typical for most rare species of high conservation priority, so simulations are used to explore the effects of dispersal, correlations in vital rates and the frequency of extreme events (*e.g.*, very "bad" years due to flooding of habitat by beaver). The simulations showed that all three factors significantly influenced the probability of quasi-extinction. However, the probability of an extreme event was most highly associated with the probability of quasi-extinction. This result suggests that future data collection should focus on capturing the frequency, duration, and intensity of extreme events for this metapopulation.

Introduction

Understanding population dynamics is a central focus of ecological theory and a central need of applied conservation biology. Demographic matrix models are a common tool used by both theoretical ecologists and conservation practitioners to describe and project population dynamics (Caswell 2001). One criticism of matrix models is that the arbitrary classification into discrete stages of continuous life cycle characteristics, such as size or age, introduces error into the models (Easterling *et al.* 2000). One proposed solution to this problem is to use algorithms that search for "optimal" stage boundaries (Vandermeer 1978, Moloney 1986). However, these methods can be difficult to carry out (Pfister and Stevens 2003) and still result in uncertainties when used to project population dynamics (Easterling *et al.* 2000). Integral projection models (IPMs) avoid the issue of defining stages of the life cycle by treating continuous variables as continuous (Easterling *et al.* 2000). Further, Ramula *et al.* (2009) showed that for two perennial herbs, IPM-based estimates of population growth (λ) had lower bias and variance than estimates derived from discrete stage-class matrix models. Most published IPM analyses have been on single populations and have not included spatial dynamics (Easterling *et al.* 2000, Ellner and Rees 2006, Ramula *et al.* 2009). There is recent interest in incorporating spatial structure in IPMs (Jongejans *et al.* 2010).

Modeling a metapopulation requires linking spatial structure to population dynamics through information such as dispersal and correlations in vital rates between patches (Akcakaya 2000). Researchers studying rare species seldom have extensive information on all of these types of data (Morris and Doak 2002). Harrison (1991) provides guidelines to help researchers determine when the complexities of a

metapopulation model incorporating spatial structure are necessary. According to Harrison's framework, a simpler single population model is preferable either when vital rates are correlated between patches or when movement rates are either extremely high or extremely low (Harrison 1991). If correlations in vital rates between patches are high and individuals at several patches go extinct, then there is little chance of recolonization (Solbreck 1991). Similarly, if dispersal between patches is high or virtually none, then rescue effects are unlikely (Brown and Kodric-Brown 1977). In such scenarios, the population dynamics are essentially those of a single population spread across multiple patches rather than those of a metapopulation (Harrison 1991).

For many rare species with high conservation priority, there are not enough data to confidently know the frequency of dispersal events and whether vital rates between patches are correlated because sampling can be destructive to populations or limited habitats. When data are limited, simulations can be a useful tool for exploring the effects of a range of dispersal probabilities and correlations in vital rates between patches to see if metapopulation dynamics are relevant to a population viability analysis. In this chapter I present a metapopulation model based on empirical data from an intensive three year study of all known extant patches of a regionally rare hemiparasitic plant, *Pedicularis lanceolata*, in Massachusetts. The *P. lanceolata* dataset suits the theoretical simulations presented here because it spans a sampling time-frame typical of many other rare species. Also, the *P. lanceolata* metapopulation model is of applied use because the information it provides will be fed immediately into adapting the management plan for the species in Massachusetts (Farnsworth *et al.* 2007), where it is listed by the state as endangered (Brumback *et al.* 1996).

Detailed data on seed dispersal rates across patches were not available for *P. lanceolata*, and even with three years of data there was not sufficient information on correlations in vital rates between patches over time. As such, I performed simulations to see how the probability of quasi-extinction of *P. lanceolata* varied in response to differences in dispersal rates and correlations in vital rates between patches. In addition, these simulations also looked at the effects of the probability of extreme events on the probability of quasi-extinction of *P. lanceolata* because in the first year of the study, flooding from beaver activity caused very low survival and reproduction at two of the patches. The beaver flooding provided information on how the vital rates of *P. lanceolata* respond to a catastrophic event, but the short duration of the study did not provide any information on the frequency of extreme events.

This chapter presents one of the first examples of a metapopulation IPM and shows how simulations can be used to determine the importance of dispersal, correlations in vital rates, and the frequency of catastrophic years when data on these variables are not available. The challenge of sparse data, even with three years of intensive sampling, is typical of rare species, so the simulations presented here are widely applicable to other species of conservation concern. Further, the methods presented here are general and can be applied to any organism whose life cycle can be described by a continuous variable such as size or age.

Methods - field data

Field data collection and a preliminary check for density dependence

Pedicularis lanceolata is a short-lived, non-clonal perennial plant (Allard 2001) that grows in periodically flooded, early successional habitats such as wet meadows,

prairies, and stream-sides (Piehl 1965, Farnsworth *et al.* 2007). The geographic range of *P. lanceolata* extends from the Midwest of North America to its eastern coast with populations as far south as Georgia and as far north as the Canadian provinces of Manitoba and Quebec (NatureServe 2010). The species is regionally rare along much of the eastern coast of the United States (NatureServe 2010). The genetic diversity of *P. lanceolata* is unknown. *Pedicularis lanceolata* is a generalist hemiparasitic species that relies on host plants to complete its life cycle (Lackney 1981). Seeds of *P. lanceolata* germinate in mid- to late spring and flowering occurs from mid-August through early September.

I collected demographic data on all known extant patches of *P. lanceolata* in the state of Massachusetts. *Pedicularis lanceolata* occurred in four patches study along a 661 m stretch of a brook in western Massachusetts and comprise a total of 4,251 separate individuals, including seedlings, over the course of the. The minimum and maximum distances between occupied patches were 50 m and 661 m, respectively. Sampling began in August of 2007 and continued until November of 2009. Each patch was extensively searched for plants in the beginning of the study, and all individuals were tagged and their locations were recorded. In late August of each year I estimated plant size as the number of leaves present and recorded the presence or absence of flowers on each plant. In October of each year, I counted the number of fruiting capsules for each plant. I collected all flowering capsules from a randomly selected subset of fifteen plants at the patch with the greatest number of plants. I then counted the number of viable seeds produced, and returned all seeds to the field scattering them below their parent plants.

Ideally seed set would have been quantified in all patches, but the study permit for this state-listed endangered species only allowed for seed collection from fifteen individuals at the most robust patch.

Additional potential habitat patches were identified in June and July of 2008. I sampled the streamside area over 13.5 km, from 6500 m downstream to 7000 m upstream from the four known patches of *P. lanceolata*. Every 50 m, within 3 m of the water's edge, I measured canopy cover with a spherical densitometer. Measurements of average percent canopy cover at patches occupied by *P. lanceolata* had 0-74% average canopy cover. Sampling points along the brook within this range of average canopy cover and at least 50 m in length were considered suitable habitat. I verified that all habitat patches categorized as suitable or unsuitable were correctly classified by cross-referencing the field-collected spherical densitometer measurements with 2005 aerial orthophotos in ArcMap version 9.3.

While there are multiple ways that *P. lanceolata* may disperse (*e.g.*, wind, water, or herbivory by highly mobile animals such as deer), a main source of dispersal for the metapopulation presented here likely is water dispersal since the plants occur in the floodplain of a brook. To quantify the frequency of flood events during which dispersal might occur, I measured water flow in the brook by placing a pressure transducer in the water adjacent to the largest patch of *P. lanceolata*. The flow measurements were taken at 15 minute intervals from the beginning of October 2009 to the end of April 2009 because *P. lanceolata* sets seed in October and November and usually germinates by the end of April. I also recorded dates when the brook was flooded enough to overtop the edge of

the bank. Cross-referencing the rates of flow on these flood days with the time-series data from the pressure transducer provided a rough estimate of the frequency of dispersal over the winter and spring of 2009.

Before proceeding with the construction of the metapopulation model, it was necessary to test for density dependence to determine if it was necessary to include density dependence in the model. Intra-specific density dependence can be inherently difficult to determine for sparse rare species. Since density dependence was most likely to be significant for patches with higher densities of individuals, I tested for density dependence in the densest patch of *P. lanceolata*, which also happened to be the largest patch. To see if the size of neighboring *P. lanceolata* within one and a half meters was a significant predictor of survival I performed a logistic regression that also included the size of the focal individual, year, and year × focal individual size interaction as predictors. A linear model was used to determine if the number of seeds produced by neighboring plants had a significant effect on the number of new seedlings per the number of seeds produced by neighboring plants.

Results - field data

Results of field data collection and density dependence check

The numbers of plants occurring in each patch in each year of the study are given in Table 4.1. Figure 4.1 shows the data collected from the pressure transducer installed in the brook along which *P. lanceolata* grows. The lowest observed measure of flow recorded during a flood event where the water level overtopped the brook's edge was 0.45 m^3 per second. In 2009 there were several flood events during which long distance seed dispersal events could have occurred.

There was some evidence of intra-specific density dependence in the largest patch of *P. lanceolata*. The size of neighboring *P. lanceolata* within one and a half meters was not a significant predictor of survival ($F_{5,894}$ = -0.043, P = 0.966) in a logistic regression that also included the size of the focal individual, year, and year × focal individual size interaction as predictors. Intraspecific density dependence did have significant effects on recruitment in the linear model analysis. The number of seeds produced by neighboring plants was significantly affected by the number of new seedlings divided by the number of seeds produced by neighboring plants ($F_{1,272}$ = 8.226, P = 0.0044).

Methods - an IPM for a metapopulation

Estimating vital rates

Vital rates for IPMs were estimated using a series of continuous functions such as linear or logistic regressions (Easterling *et al*. 2000). Six variables were estimated for *P. lanceolata*: growth, fecundity, and seedling size, and probabilities of survival, flowering, and seedling establishment. In all models, year was treated as a fixed effect, as recommended by Rees and Ellner (2009) for the analysis of short-term datasets. To begin, all of the analyses used to model the vital rates were done on the pooled dataset containing all occupied patches and years (full results in Table 4.2). These initial analyses were used to make decisions about the most appropriate models for the vital rates that were then used in the metapopulation IPM. If the fixed effects of year or patch were found to be significant when analyzing the entire dataset, then separate patch or year analyses were also carried out for the patch of interest. Table 4.3 summarizes the models used to estimate these rates. The size values used in these models corresponded to the range of observed sizes. The assumption that most demographic rates are identical across

patches while only a few vary is a common approach to dealing with limited data in a metapopulation viability analysis (Porneluzi and Faaborg 1999, Morris and Doak 2002). One patch was excluded from the separate patch analyses because it contained only one plant during the study.

Survival

Survival probability was modeled using logistic regression with size *x* at time *t* as the predictor variable (Table 4.2, Fig. 4.2). Annual survival depended on size *x*, year, and patch (Table 4.3). When the numbers of successes or failures in the odds ratio were less than two and/or when the sample sizes at a patch were low, the regression coefficients had inflated standard errors. It was problematic to have standard errors greater than the parameter estimates because the standard errors of the coefficients were needed later to model observation error in the vital rates. Such inflated standard errors would have yielded unrealistic vital rate estimates, such as probabilities of survival greater than one. Thus, when the standard errors of the regression coefficients exceeded the mean, data with all three patches pooled for a given year were used. The slope was adjusted by multiplying it by the number of surviving individuals at time t+1 and dividing by the number of individuals observed at time *t*.

Size of recruits and growth

Mean seedling size was not dependent on year or patch (Table 4.3) and so a normal distribution truncated at zero was used to model it (Table 4.2, Fig. 4.3). Annual growth was modeled as a linear model with size-dependent variances (Table 4.2, Fig. 4.4). Yearly changes in plant size were dependent on size in the previous year *x*, but not dependent on year or patch (Table 4.3).

Flowering and seed production

The probability of flowering was dependent on size *x* and patch, but not on year (Table 4.3), so flowering probability was modeled as a logistic regression with size *x* at time *t* as the predictor variable (Table 4.2, Fig. 4.5). There were significant effects of year and size *x*, but not patch, on seed production (Table 4.3). Seed production was modeled using a Poisson regression with size *x* as the predictor variable (Table 4.2, Fig. 4.6). The number of seeds produced per plant was calculated as the number of fruiting capsules multiplied by the average number of seeds per capsule based on the yearly seed data collected on 15 plants from the most robust patch. I estimated the probability of establishment (*i.e.*, recruitment – here I remain consistent with the terminology used in previous published IPMs) as the ratio of seedling recruitment to seed production at each patch for each year of the study (Ellner and Rees 2006).

Model structure

A single patch IPM inputs the distribution of plants of size *x* at time *t* and predicts the distribution of individuals of size *y* in time *t* + 1 by

$$n(y) = \int_{\Omega} [p(x,y) + f(x,y)]n(x)dx \quad (1)$$

where *p(x,y)* and *f(x,y)* are survival-growth and fecundity kernels, respectively, that describe all of the transitions from plants of size *x* to size *y* over all possible sizes (Ω) (Easterling *et al.* 2000). The survival-growth kernel can be expanded to

$$p(x,y) = s(x)g(x,y) \quad (2)$$

where *s(x)* is the probability of an individual of size *x* surviving to become a plant of size *y*, and *g(x,y)* is the probability of a plant of size *x* growing to size *y* (Easterling *et al.* 2000). The fecundity kernel is

$$f(x,y) = p_f(x)\, f_n(x) f_d(y) p_{est} \qquad (3)$$

where $p_f(x)$ is the probability that a plant of size x flowers, $f_n(x)$ is the number of seeds produced by an individual of size x, $f_d(y)$ is the size distribution of recruits, and p_{est} is the probability that a seedling establishes (Rees and Ellner 2009). As in other studies (Childs *et al.* 2003, Rose *et al.* 2005), this model makes the necessary simplification that maternal plant size and offspring size are not related.

Usually, survival-growth and fecundity kernels are summed to yield a single kernel, $k(x,y)$, which is then used to iterate the model or to perform sensitivity analyses (Ellner and Rees 2006). By keeping the survival-growth kernel and the components of the fecundity kernel separated, along with tracking the dispersal of seeds, a metapopulation IPM can be constructed. Figure 4.7 outlines the progression of steps implemented in the *P. lanceolata* metapopulation IPM. First, the vital rates were estimated as described in the previous section. Second, a set of vital rates for each patch was selected (in the *P. lanceolata* IPM, vital rates were only estimated for three of the four patches because one patch had only one individual). Thus, for each patch during each time step I selected from vital rates for each of the six possible patch-year combinations (patch one, 2007-2008; patch one, 2008-2009; patch two, 2007-2008, *etc.*). With a dataset spanning more years, vital rates could be selected for the patch from different years from which they were originally estimated. To incorporate observation error into each set of vital rates, the regression coefficients were sampled from normal distributions with means and standard deviations equal to those listed in Table 4.3.

Third, the survival-growth kernel ($p(x,y)$) and the components of the fecundity kernel ($f(x,y)$) were calculated (Fig. 4.7). The survival-growth kernel for the multi-patch IPM (referred to hereafter as **PD** in keeping with the notation used in the first IPM by Easterling *et al.* 2000) was a square matrix with 100 rows and 100 columns. To determine the appropriate dimensions for **PD** (*i.e.*, the number of mesh points needed for numerical integration), I selected the smallest matrix that when projected produced similar values of the population growth rate (λ) compared to larger matrices (Ellner & Rees 2006, Fig. 4.8). The components of the fecundity kernel representing the probability of flowering, $p_f(x)$, and seed production, f_n, were multiplied in a function called seeds(x). The parameters of the fecundity kernel for seedling size, $f_d(y)$, and the probability of establishment for recruits, p_{est}, were multiplied to form a vector referred to as **KIDD**, which refers to the recruits produced by the adults accounted for in the survival-growth kernel, **PD**.

To get the size distribution of the number of seedlings and non-seedlings at time $t + 1$, **KIDD** and **PD** were used. In the fourth step, the number of seeds at time t, $seeds_t$, at a given patch was multiplied by the vector **KIDD** resulting in a vector containing the size distribution of recruits at time $t + 1$ (Fig. 4.7). The number of elements in this vector equaled the number of mesh points (in this example 100). As the starting values for the number of seeds per patch, I used estimates of the number of seeds per patch in 2009, the last year of data collection, based on multiplying the average number of seeds per capsule by the observed number of capsules per plant. In the fifth step, the **PD** matrix was multiplied by a vector of the size distribution of total plants at time t, $\mathbf{N}_t$. The starting values for each patch's **N** vector were the number of individuals in each size category in

2009. The sum of the two vectors of size distributions of seedlings and non-seedlings at time $t + 1$ gave the size distribution for all plants at a patch in time $t + 1$, which then was used as the input for the next iteration.

The sixth step determined the number of seeds staying within a patch or dispersing between patches. The vector $\mathbf{N}_t$ was input into the function seeds(x). The sum of the resultant vector rounded to the nearest whole number gave the total number of seeds produced that were capable of remaining within a patch or dispersing between patches in the next time step. Multiplying this total number of seeds produced by a patch × between-patch dispersal probability matrix generated a matrix whose row sums equaled the inputs of seeds for each patch in the next iteration. For *P. lanceolata* there was not sufficient data on the probabilities of dispersal distances, so I used a range of values, as described in the next section, to see how different dispersal rates and probabilities affected the probability of extinction. After the sixth step for each patch, the first time step was complete and the model was iterated with the new inputs generated for the number of seeds and the size distribution of plants.

Incorporating intra-specific density dependence

Since preliminary analyses showed that there were significant effects of intra-specific density dependence on *P. lanceolata* in Massachusetts, density dependence was included in the metapopulation model. To relate density of seeds to density of seedlings I parameterized a nonlinear least squares model. From this function, the density dependent probability of establishment was predicted and scaled to the observed probability of establishment (number of seedlings/number of seeds) for a given transition. This approach made it possible to change the probability of establishment based on the

number of adult plants in a habitat patch. A ceiling was also included on the number of plants per habitat patch. To calculate the ceiling, I took the maximum observed number of plants per 1 m × 1 m (110 plants) and multiplied it by the size of the habitat patch (see description of habitat patch sizes below).

Simulating the effects of dispersal, correlations in vital rates between patches, and the frequency of extreme events on the probability of quasi-extinction

Simulations were used to see how the probability of quasi-extinction of *P. lanceolata* varied in response to differences in dispersal rates, correlations in vital rates between patches, and the frequency of extreme events (*e.g.*, flooding of habitat by beaver). In all simulations, the quasi-extinction threshold for the entire population was 100 individuals. A quasi-extinction threshold of 100 genets is a reasonable number for maintaining genetic diversity (Morris and Doak 2002). If the total number of plants across all patches fell below 100 individuals at any time during a 50-year simulation, then the population was considered to be extinct.

Because *P. lanceolata* in this population grows only along a brook and within its floodplain, long-distance dispersal of seeds between patches likely occurs via the movement of water. The stream length of the patch size used in the model is 50 m, the resolution available from field sampling for suitable habitat. The effects of dispersal in metapopulation models can be sensitive to variable patch sizes (Collingham and Huntley 2000), but the patch size used in this model was not varied. The objective of this study was to explore the sensitivity of quasi-extinction to factors such as dispersal, correlations in vital rates between patches, and the frequency of extreme events rather than to predict population dynamics, so the fixed patch size of 50 m seemed sufficient.

Seed dispersal was modeled as a one-dimensional inverse power function, where the center of the patch producing seeds was at zero on the *x*-axis and the *y*-axis was the probability of dispersal for seeds at distance *x*. The first 25 m along the *x*-axis of the dispersal curve were seeds that dispersed into the parent patch. The remaining area under the dispersal curve, for distances greater than 25 m along the *x*-axis, integrated to one. Technically this is an improper integral, since the curve is unbounded, but this approach works in the limit. Distances along the brook from the center of one patch to the center of another were known from field measurements. To calculate the number of seeds dispersing between patches, I summed the area under the dispersal curve for a patch of length 50 m centered at the distance between the two patches, then multiplied that number by the probability of dispersal. Given the unidirectional flow of water, 90% of dispersing seeds were modeled to move downstream. Ten percent of dispersing seeds were able to move upstream since there is some probability that seeds could move in that direction (*e.g*, if deer eat the seeds and then walk upstream and deposit them there).

To model the probability of positive correlation in vital rates between patches, at the beginning of each time step one set of vital rates was randomly selected from the six sets of vital rates corresponding to the three patches with > 1 individual and the two annual transitions. This first set of vital rates was considered as a reference for the selection of subsequent sets of vital rates. Random draws from a binomial distribution with a probability stepping through the range from zero (no correlation in vital rates between patches) to one (complete correlation in vital rates between patches) determined whether or not subsequent sets of vital rates would match the initial set of vital rates or not. In addition to modeling the probability of positive correlation in vital rates between

patches, there was a separate component in the model for spatial auto-correlation between patches. Spatial auto-correlation was modeled as a Gaussian process with a mean of 0.5 and a standard deviation of 100. This function resulted in probabilities of spatial auto-correlation that quantitatively matched field observations: for example, during flood events caused by beavers, patches within 100m had similar dynamics but correlations between vital rates decreased with distance for patches > 100m apart.

In 2007, the first year of the study, flooding from beaver activity caused very low survival and reproduction in two of the patches. Although beaver had activity had a negative effect on survival and reproduction during the sampling period of this study and this model treats these low values of survival and reproduction as negative, it is noteworthy that beaver activity also maintains the sunny habitat needed for *P. lanceolata's* persistence. The beaver flooding provided information on how the vital rates of *P. lanceolata* responded to an extreme event, but the short duration of the study did not provide any information on the frequency of such events. The probability of an extreme event was modeled with a binomial distribution. Three of the sets of growth rates indicated declining populations ($\lambda = 0.20, 0.70, 0.71$), and three indicated increasing populations ($\lambda = 1.8, 3.67, 3.68$). A binomial draw for each patch at each time step determined whether or not the set of vital rates selected was from the sets with population growth rates below one ("extreme") or not.

To assess the effects of dispersal, correlations in vitals rates, and the frequency of extreme events on the probability of quasi-extinction, simulations were run for 16 levels of each predictor variable. Sixteen levels were used to balance computational time with the number of points needed for subsequent linear regression analyses. Dispersal

probabilities used in the model ranged from 0.0001 to 1 on a $\log_{10}$ scale. The probabilities of positive correlations in vital rates ranged from 0 to 1. The probabilities of extreme years in the simulations ranged from 0 to 0.7. I used this range because initial analyses showed that independent of the probabilities of dispersal or positive correlations in vital rates, the probability of extinction was equal to 1 when the probability of an extreme event was > 0.7.

The overall analysis included 163,840 simulations (40 repetitions × 16 levels each for probabilities of dispersal, positive correlations, and extreme events). I used multiple linear regression to determine how the three predictors (*i.e.*, dispersal, correlations in vital rates, and the frequency of extreme events) influenced the probability of quasi-extinction. The results of the linear model were then analyzed with hierarchical partitioning using the 'hier.part' package in R statistical software to determine the relative importance of each predictor to the probability of quasi-extinction. Hierarchical partitioning evaluates how the fit of a model (*e.g*, r^2) with a particular predictor compares to a model without the predictor. Hierarchical partitioning separates the total r^2 for each predictor into two additive components 1) the independent contributions of the predictor and 2) the joint contributions of each predictor in conjunction with other predictors (Quinn and Keough 2002). All analyses were performed using R statistical software version 2.10.1 (R Development Core Team 2010).

Results - an IPM for a metapopulation

The probabilities of an extreme event, positive correlations in vital rates between patches, and dispersal all had significant effects on the probability of quasi-extinction (Table 4.4). When the probability of extreme events was less than ~0.05 the quasi-

extinction probability was essentially none, but when the probability of extreme events exceeded 0.5 quasi-extinction was inevitable (Figs. 4.9 and 4.10). As the probability of positive correlation in vital rates increased, the probability of quasi-extinction increased (Fig. 4.10). The response of the probability of quasi-extinction to the probability of dispersal was slightly modal with intermediate probabilities of dispersal having a higher probability of quasi-extinction when the probability of positive correlation was less than 0.6 (Fig. 4.10). The interaction between correlations in vital rates and the frequency of extreme events was significant, with extreme events having a more negative effect on the probability of quasi-extinction when vital rates were highly correlated (Table 4.6).

Results of the hierarchical partitioning analysis indicated that the probability of extreme years, relative to the other predictor variables, had the largest independent contribution to the probability of quasi-extinction (Table 4.5). The joint contributions of each predictor variable coincident with other predictors were low, suggesting that the predictor variables were uncorrelated with one another (Table 4.5) (Quinn and Keough 2002).

Discussion

Metapopulation models require extensive information on dispersal, patch-specific demography, and correlations in vital rates between patches (Hanski *et al.* 1995, Akcakaya 2000), yet researchers seldom have sufficient data to confidently estimate all of these parameters (Harrison 1991, Morris and Doak 2000). In this chapter I have described how field data and simulation models together can be used to explore the effects of dispersal, correlations in vital rates across patches, and frequencies of extreme events on metapopulation dynamics when data on these variables are limited. In addition,

this paper presents one of the first uses of IPMs for metapopulations (Jongejans 2010), and illustrates how they can be used to project population dynamics similar to a multi-patch matrix model, but without the issues associated with forcing continuous variables, such as size or age, into a set of discrete classes (Easterling 2000).

The probabilities of positive correlation, dispersal, and extreme events all had significant effects on the probability of quasi-extinction. As the probability of positive correlations in vital rates across patches approached one, the probability of quasi-extinction increased because patches were likely to be hit simultaneously by extreme events, thus decreasing the possibility that rescue and re-colonization from an unaffected patch would occur. Conversely, as the probability of positive correlations in vital rates decreased the probability of quasi-extinction decreased. This results supports the ideas that metapopulation models should consider a range of correlations in vital rates (Lahaye *et al.* 1994, McCarthy and Lindenmayer 2000) and that PVAs with no positive spatial correlations tend to be overly optimistic (Morris and Doak 2000).

The probability of quasi-extinction was also affected by dispersal. While the data on flood events from the pressure transducer provided some evidence of the frequency of high water events that could result in long distance dispersal of seeds by water, it was difficult to calculate probabilities of dispersal from the data. Dispersal here was modeled as an inverse power function with a fat tail, but this distribution may overestimate dispersal if the tail of the dispersal curve is actually thinner (Jongejans *et al.* 2008). However, more empirical information on the multiple processes driving seed dispersal of *P. lanceolata* (*e.g.*, animal or water-mediated movement) are needed to determine the

shape of the tail of the dispersal kernel (Wang 2002). The IPM presented here is flexible, so that with additional data on seed movement between patches, different dispersal functions could be incorporated easily.

The probability of extreme events also had a significant negative effect on the probability of quasi-extinction (Fig. 4.10). The plants in two of the occupied patches experienced low survival and reproduction in 2007 due to flooding of the streamside by beaver dams. The definition of annual transitions with $\lambda << 1$ as extreme "bad" events in the simulations seemed reasonable because at these two patches the population growth size dropped from hundreds of individuals to just a few plants in 2007. Ironically, beavers create the open sunny habitat in which *P. lanceolata* thrives, and management plans for *P. lanceolata* in New England identify succession of woody vegetation as another threat to this endangered species (Allard 2001, Farnsworth *et al.* 2007). In this model, beaver activity is treated as an extreme negative event, but beaver are important ecosystem engineers in this system, they maintain the early successional habitat needed by *P. lanceolata.* The data from these simulations suggest that the management of beaver activity along the brook will have a strong impact on the persistence of *P. lanceolata*. The management implications of this result are that *P. lanceolata* habitat must be managed both for hydrologic regimes where inundation is not persistent during the growing season and for high light availability.

This balance of disturbance regimes is also seen for a geographically close congener of *P. lanceolata*, the Maine endemic, *P. furbishiae*. The persistence of the *P. furbishiae* metapopulation depends upon the maintenance of open disturbed patches

created by ice scouring the banks of the St. John River in the winter, but excessive ice scour leads to erosion that destroys the narrow strips of riverside land on which *P. furbishiae* grows (Menges 1990).

The probability of extreme events had a much greater contribution to the probability of quasi-extinction than did the probabilities of dispersal or positive correlations in vital rates (Table 4.5). This result suggests that close attention should be paid to collecting data on the frequencies, durations, and intensities of future or historic catastrophic events. Further, if funds for sampling are limited, it would be more worthwhile to gather data on the frequencies of catastrophes than to collect more data on seed dispersal.

When assessing the results of this simulation, it is important to consider some inherent limitations of the parameterization of the model. The identification of suitable habitat patches for the model was based on percent canopy cover along the brook, but there are probably many other abiotic and biotic factors that constrain the distribution of *P. lanceolata*, including land-use history, hydrology, and the availability of suitable host plants (Allard 2001). *Pedicularis lanceolata* is a generalist hemiparasitic species that parasitizes both native and invasive species, and greenhouse and field removal studies have shown that *P. lanceolata* growth and survival are higher when it is attached to native rather than invasive species (Chapter II). Quantification of suitable habitat for *P. lanceolata* based on the abundances of native and invasive host plants would yield fewer patches of available habitat, so the results of this simulation might be optimistic because migration rates can be affected by patch density (Hanski 1995). The patches specified in

the simulation were also of the same size because finer scale data were not available. Varied patch sizes could also affect the results of the simulation (Collingham and Huntley 2000).

Another limitation, or potential asset, of the data used to parameterize the model is that the years spanned by the data are likely to have been extremely "good" and "bad" years as evidenced by values of the population growth rate (λ) much greater or much less than one. Concern has been raised regarding PVAs based on short time series of data. (Hamilton and Moller 1995, Taylor 1995, Ludwig 1999). If the years of data collection do not span the range of environmental variation experienced by the species being modeled, then the estimates of vital rates and the models derived from them will not be representative of the actual population dynamics. One challenge of the extreme years spanned by the *P. lanceolata* dataset is that the time-series of the data is not long enough to shed light on the temporal correlations in extreme events. However, the extreme years spanned by the data set also provide the unique opportunity to explore how the probability of a very "bad" year influences the probability of quasi-extinction.

Finally, the model does not incorporate seed bank dynamics. Without knowledge of seed bank dynamics, it is difficult to confidently parameterize models of colonization, re-colonization, and extinction (Freckleton and Watkinson 2002). However, with more detailed data on seed germination and death, a discrete-state variable for the number of seeds in the seed bank could be added to the model (Ellner and Rees 2006).

These limitations are specific to the short-term data set on *P. lanceolata* and should not detract from the major contribution of this paper: one of the first applications of IPMs to metapopulation dynamics. The purpose of the simulation is to show how a

metapopulation IPM can be used to see how dispersal, correlations in vital rates, and the frequency of catastrophic events influences the probability of quasi-extinction for a limited data set typical of many species of conservation concern. The metapopulation IPM is not restricted to such exploratory data analysis, and with a richer data set it could be used to project population dynamics with less uncertainty than a discrete, matrix-based PVA.

Table 4.1. Number of *P. lanceolata* genets growing in each patch from 2007-2009. The patch numbers correspond to the naming system used by the Massachusetts Natural Heritage and Endangered Species Program.

Patch	2007	2008	2009
2	98	4	281
4	6	16	105
5	1956	1120	856
6	1	1	1

Table 4.2. Results of tests for year and patch effects on the vital rates of *P. lanceolata*. A * denotes statistical significance where $\alpha = 0.05$.

Response	Model	Effect	*d.f.*	M.S.	*F*	*P*
Growth	Linear regression	Size	1	131.70	185.45	<0.0001*
		Patch	1	7.70	10.87	0.001*
		Year	1	0.19	0.26	0.61
		Residual	817	0.71		
Survival	Logistic regression	Size	1	8.61	86.82	<0.0001*
		Patch	1	41.68	420.04	<0.0001*
		Year	1	52.02	52.02	<0.0001*
		Residual	830	0.10		
Flowering	Logistic regression	Size	1	85.134	675.30	<0.0001*
		Patch	1	2.832	22.46	<0.0001*
		Year	1	0.04	0.33	0.5675
		Residual	830	0.126		
Fecundity	Poisson regression	Size	1	93739308	22.97	<0.0001*
		Patch	1	402884	0.10	0.75
		Year	1	87545607	21.45	<0.0001*
		Residual	495	4081713		
Seedling size	ANOVA	Year	1	0.10	0.68	0.41
		Patch	1	0.46	3.1	0.08
		Residual	685	0.15		

Table 4.3. Statistical models and parameter estimates for the vital rates of *P. lanceolata*. The models are functions of *ln*(total leaves per plant + 1). Sizes at time t and t+1 are denoted by x and y, respectively. Values in parentheses following mean parameter estimates are the corresponding standard errors. A * indicates models where the data were not separated by year because year effects were not significant. Unless otherwise specified, data were pooled for all patches. A † denotes logistic regression models where the pooled patch data for separate years with adjusted slopes were used when variance was high on the partitioned patch data.

Vital rate	Model
Growth	*$\bar{y}$ = 2.38(0.10) + 0.44(0.03)x, variance about the growth curve, σ^2 = 0.56 exp(0.11$\bar{y}$)
Survival probability	†2007-2008, Patch 2: Logit(s) = -1.13(0.36) + 0.01(0.007)x †2007-2008, Patch 4: Logit(s) = -1.13(0.36) + 0.27(0.21)x 2007-2008, Patch 5: Logit(s) = -0.93(0.41) + 0.23(0.14)x †2008-2009, Patch 2: Logit(s) = 5.70(1.64) + 0.39(0.33)x †2008-2009, Patch 4: Logit(s) = 5.70(1.64) + 0.41(0.34)x †2008-2009, Patch 5: Logit(s) = 5.70(1.64) + 0.37(0.34)x
Flowering probability	*Patch 2: Logit(p_f) = -.475(1.05) + 1.61(0.36)x *Patch 4: Logit(p_f) = -17.38(4.23) + 5.79(1.51)x *Patch. 5: Logit(p_f) = -11.46(0.52) + 3.38(0.17)x
Fecundity (seeds per flowering plant)	2007-2008: f_n = exp(-2.86(0.04) + 1.85(0.01)x) 2008-2009: f_n = exp(5.39(0.01) + 0.39(0.002)x)
Probability of seedling establishment	2007-2008, Patch 2: p_e = 0.00 2007-2008, Patch 4: p_e = 0.001 2007-2008 Patch 5: p_e = 0.013 2008-2009, Patch 2: p_e = 0.001 2008-2009, Patch 4: p_e = 0.005 2008-2009, Patch 5: p_e = 0.013
Distribution of seedling size	*2007-2008 & 2008-2009: Gaussian truncated at 0 with mean = 2.38 and variance = 0.10

Table 4.4. Results of tests for year and patch effects on the vital rates of *P. lanceolata*. A * denotes statistical significance where $\alpha = 0.05$.

Response	Model	Effect	*d.f.*	M.S.	*F*	*P*
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		Patch	1	7.70	10.87	0.001*
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		Patch	1	2.832	22.46	<0.0001*
		Year	1	0.04	0.33	0.5675
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		Patch	1	402884	0.10	0.75
		Year	1	87545607	21.45	<0.0001*
		Residual	495	4081713		
Seedling size	ANOVA	Year	1	0.10	0.68	0.41
		Patch	1	0.46	3.1	0.08
		Residual	685	0.15		

Table 4.5. Results from the multiple linear regressions on the response of the probability of extinction to the probabilities of dispersal, positive correlations in vital rates between patches, and the frequencies of catastrophic events for the two patch availability scenarios. A * denotes statistical significance where $\alpha = 0.05$.

Parameter	Estimate	Standard error	*t*	*P*
Intercept	-0.224	0.024	-9.255	<0.0001*
Extreme event	3.27	0.060	54.29	<0.0001*
Dispersal	-0.028	0.010	-2.643	0.008*
Correlation	0.283	0.041	6.864	<0.0001*
Extreme event × dispersal	0.025	0.026	0.974	0.330
Extreme event × correlation	-0.337	0.103	-3.278	0.001*
Dispersal × correlation	0.025	0.018	1.416	0.157
Extreme event × dispersal × correlation	-0.022	0.045	-0.489	0.625

Table 4. 6. Results from the hierarchical partitioning analyses for the multiple linear regressions on the response of the probability of extinction to the probabilities of dispersal, positive correlations in vital rates between patches, and the frequencies of catastrophic events for the two patch availability scenarios.

Predictor variable	Independent contribution	Joint contribution	Total contribution
Dispersal	3.55×10^{-4}	5.35×10^{-17}	3.55×10^{-4}
Correlation	3.54×10^{-3}	-4.29×10^{-17}	3.54×10^{-3}
Extreme events	0.877	0.000	0.877

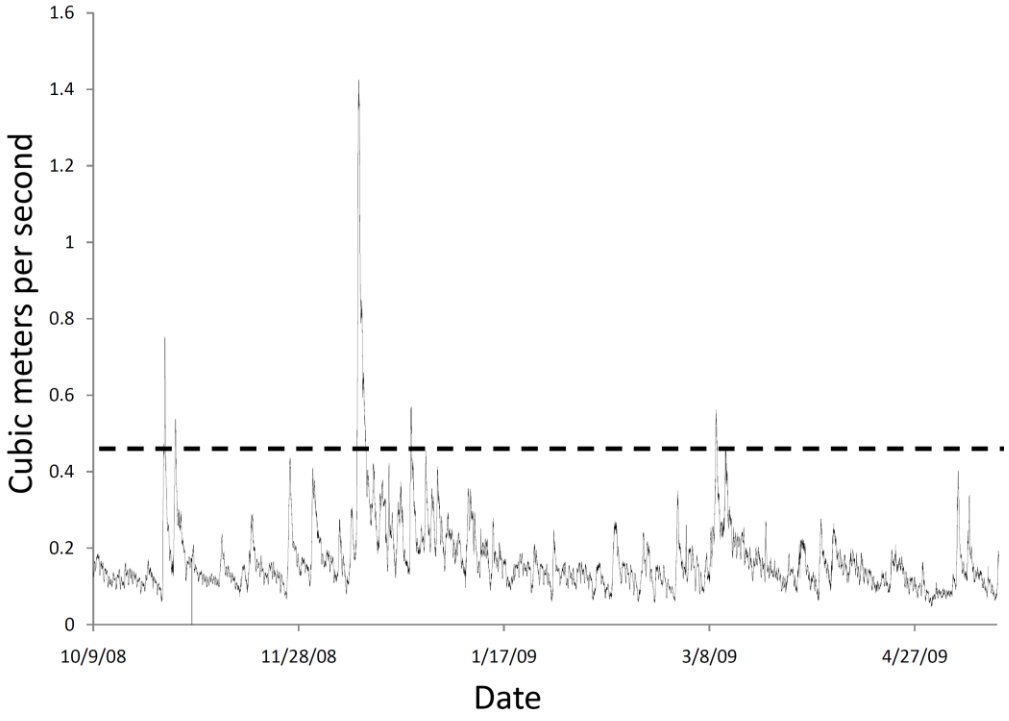

Figure 4.1.The number of cubic meters per second flowing through an area of the brook along which *P. lanceolata* grows from October 2008 through May 2009. Values above the dotted line indicate levels of flow high enough for water to overtop the brook's bank and potentially generate long distance seed dispersal events.

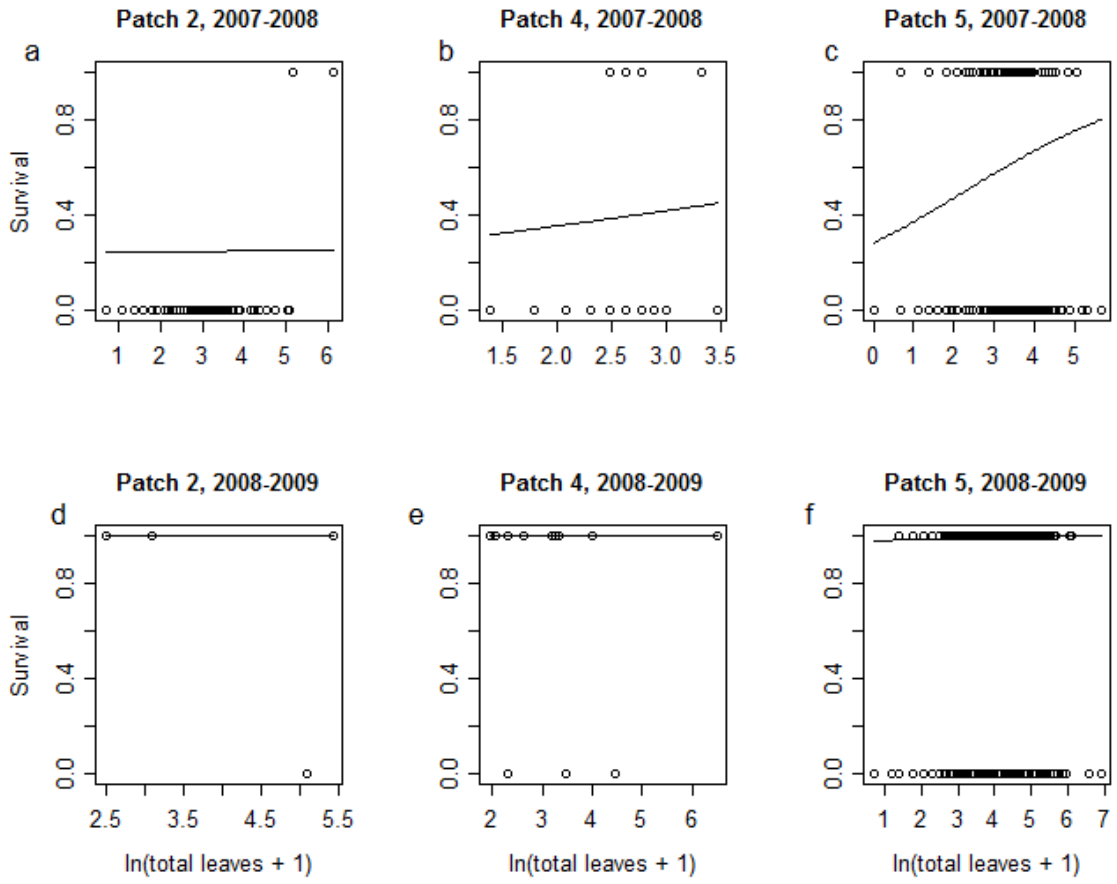

Figure 4.2. Survival estimates in 2007-2008 for the three patches are shown in a-c. Separate logistic regressions were fit for each patch in each year. Survival estimates in 2008-2009 for the three patches are shown in d-f.

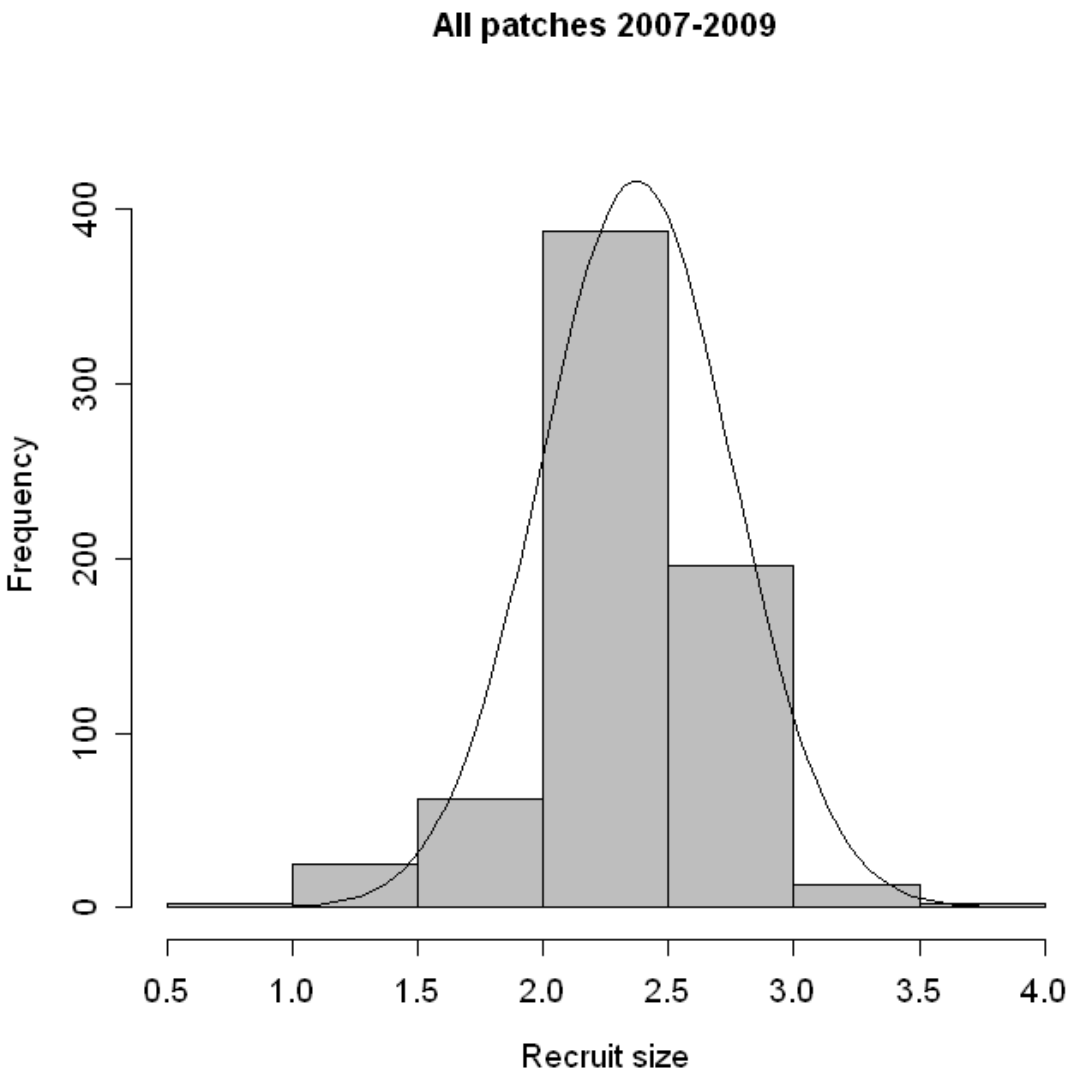

Figure 4.3. Estimated recruit size *ln*(total leaves + 1) for all patches from 2007-2009.

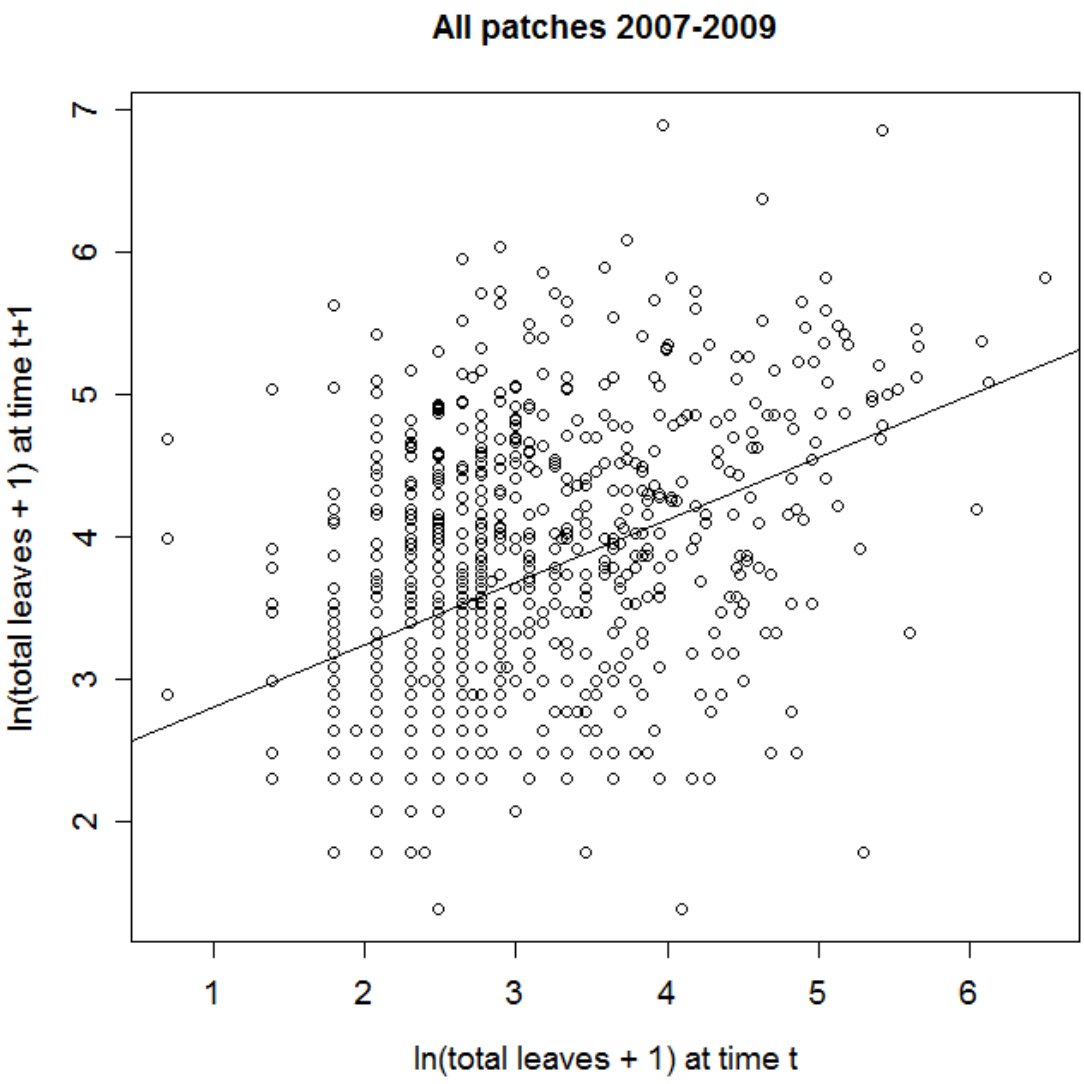

Figure 4.4. Estimates of growth for all patches from 2007-2009.

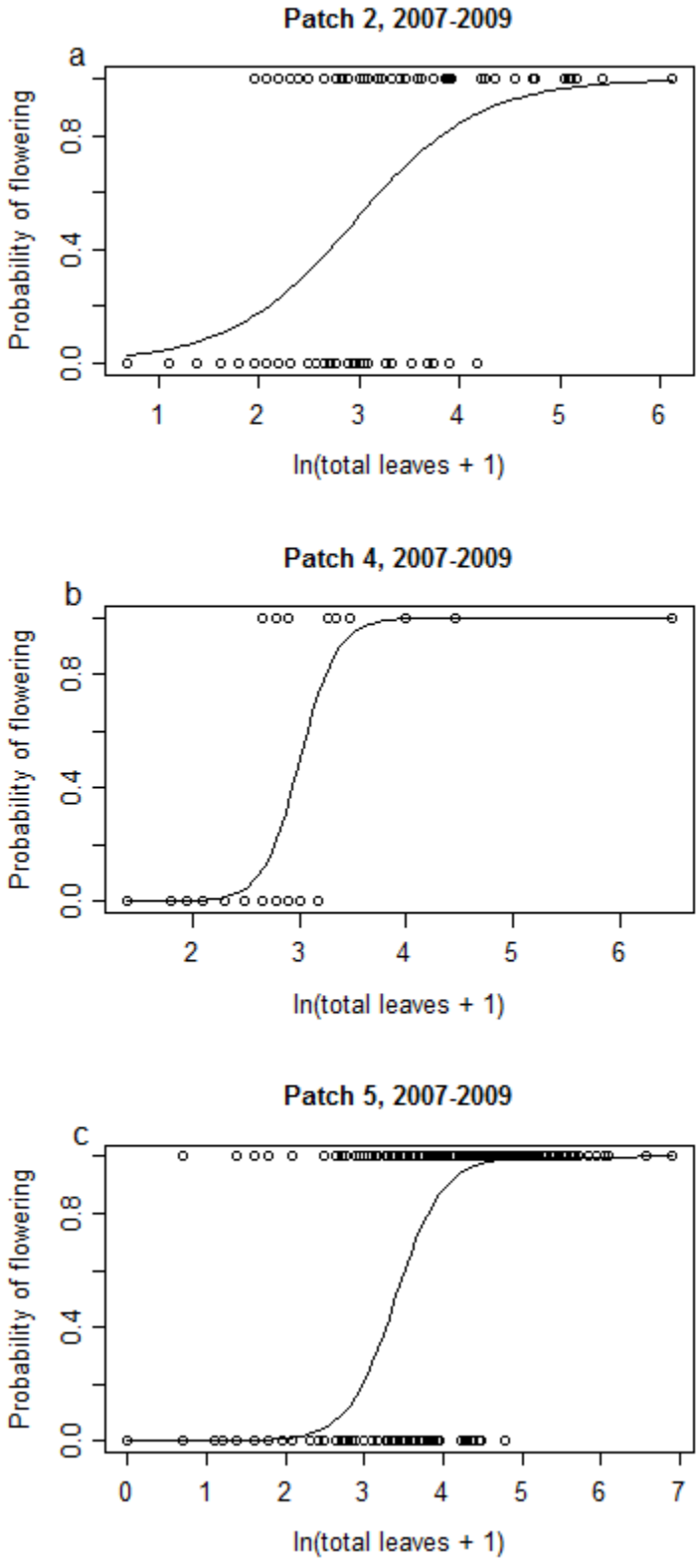

Figure 4.5. Logistic regressions for the probability of flowering for each of the three patches from 2007-2009.

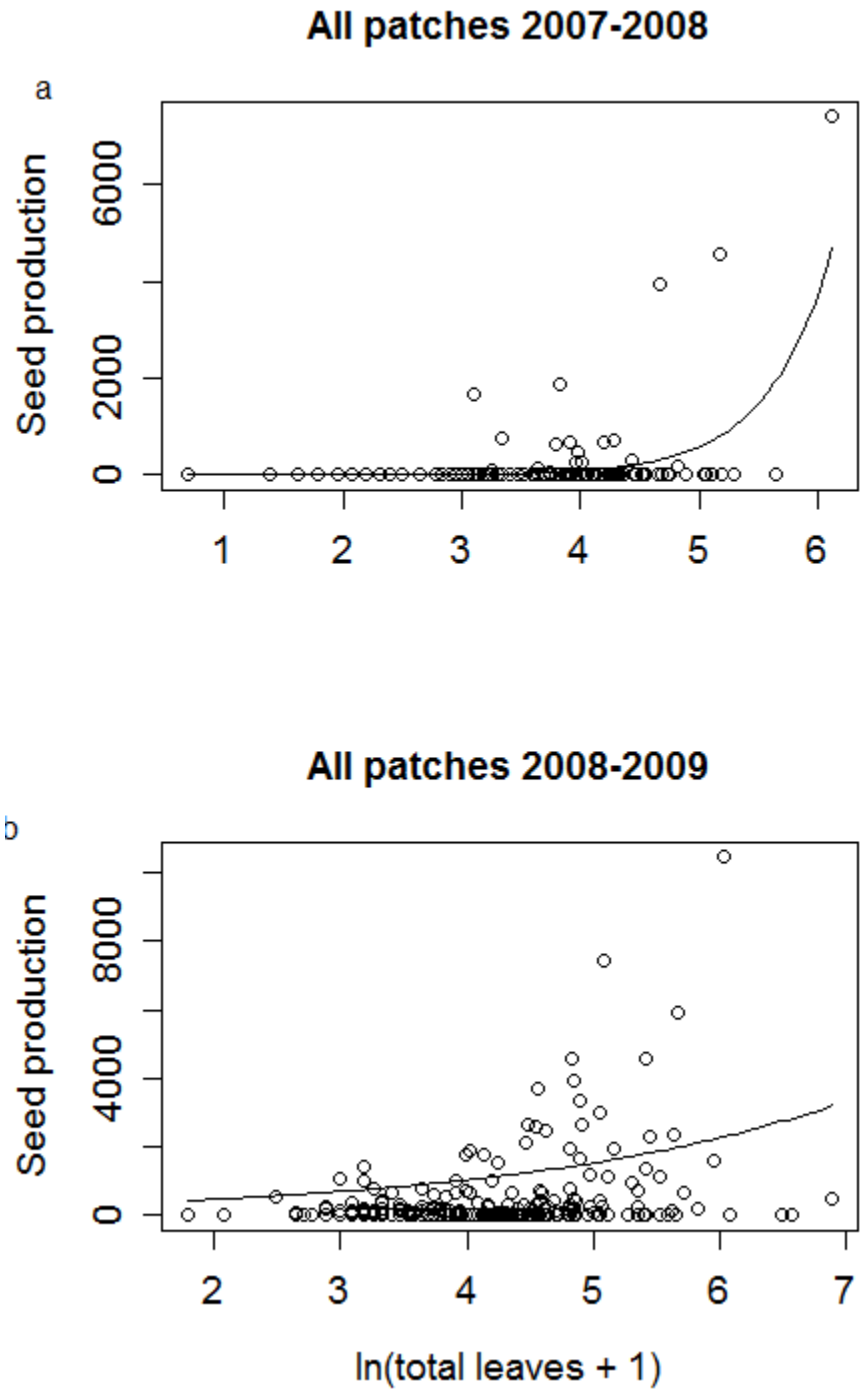

Figure 4.6. Poisson regression estimates of seed production as a function of plant size for all three patches in 2007-2008 and 2008-2009.

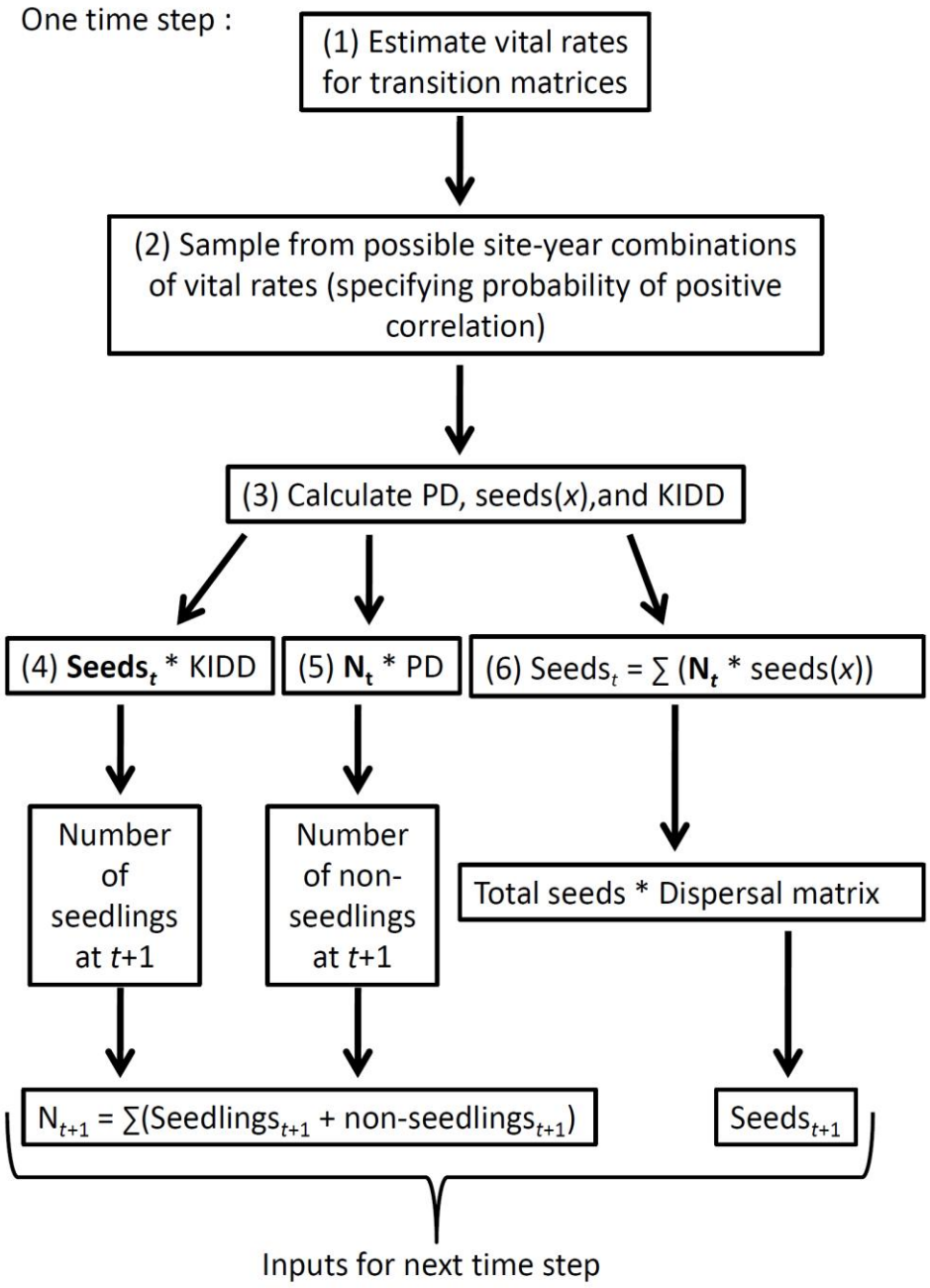

Figure 4.7. Progression of steps in a single iteration from time *t* to time *t*+1 of the metapopulation IPM. Where N_t is the size distribution of individuals and $seeds_t$ is the number of seeds at a patch at time *t*. The matrix **PD** is the survival-growth kernel, the vector **KIDD** converts the number of total seeds into the number of offspring of a given size produced by a patch, and seeds(*x*) is a function that calculates the number of seeds of produced by a patch given N_t.

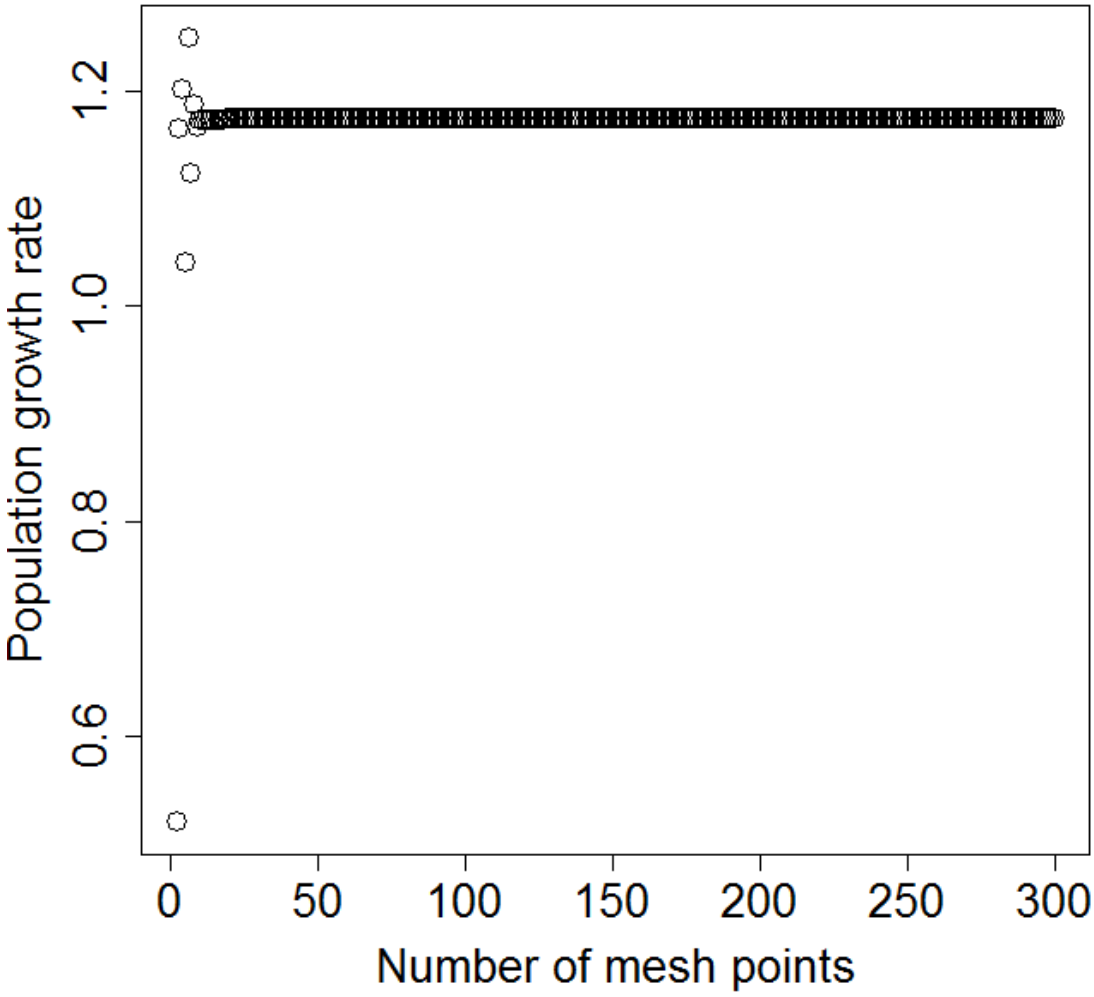

Figure 4.8. This graph shows the number of mesh points needed to reach stable estimates of the population growth rate (λ) for the largest patch of *P. lanceolata.* Stable estimates of λ were reached at approximately 50 mesh points for all patches for all years of data. The number of mesh points used for all simulations was 100.

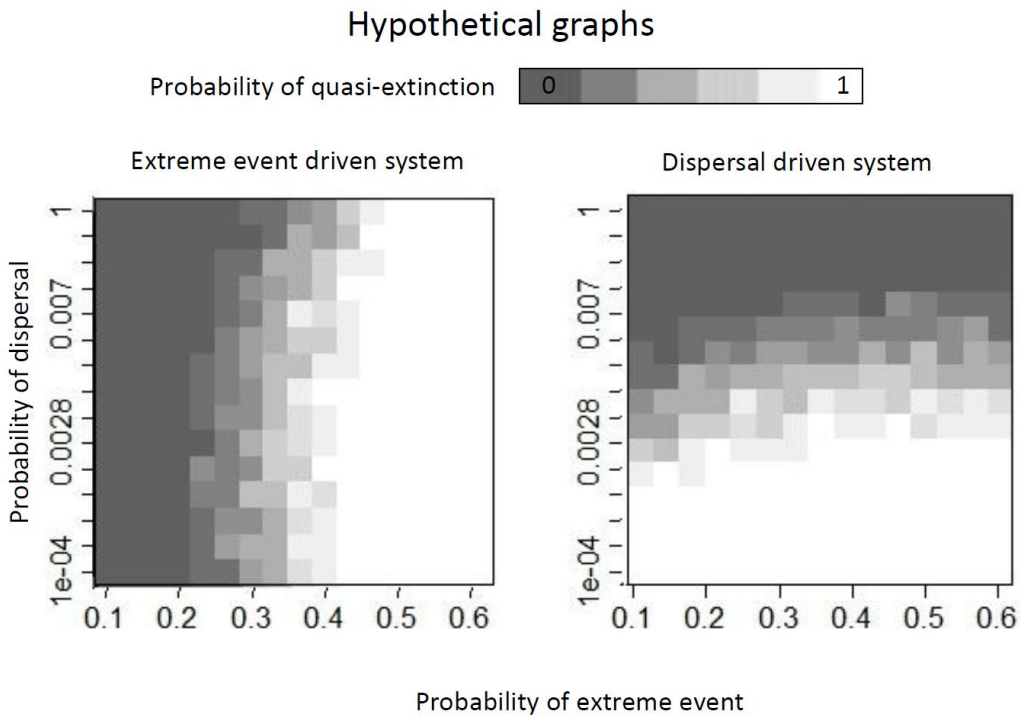

Figure 4.9. These graphs show hypothetical results from the simulation analyses to aid in the interpretation of the real results. Low and high probabilities of quasi-extinction are depicted by dark and light shading, respectively. If metapopulation dynamics are driven by extreme events, the gradient from dark to light would be left to right. Conversely, if metapopulation dynamics are driven by dispersal, then the gradient from dark to light would be from top to bottom.

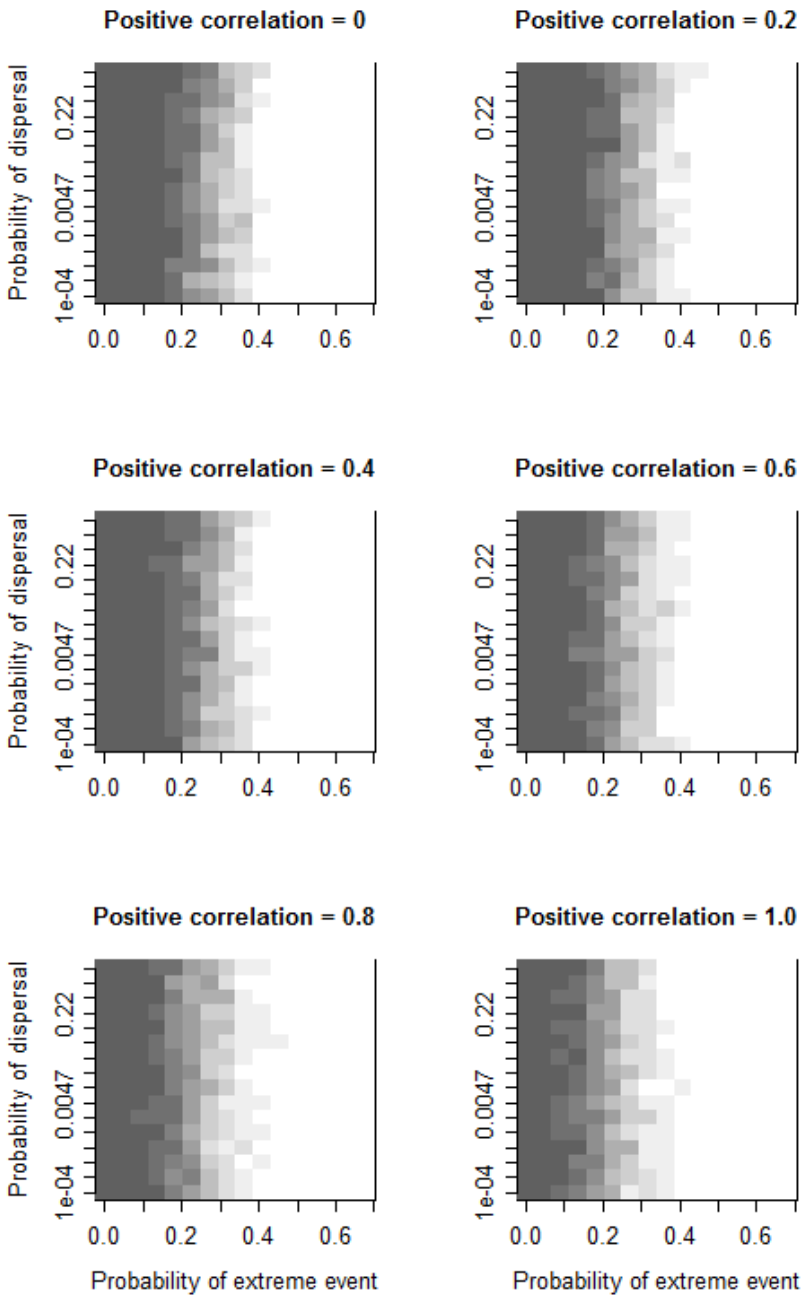

Figure 4.10. These contour plots show the results of the simulations assessing the effects of the probabilities of dispersal, of positive correlations in vital rates, and of catastrophic events on the probability of quasi-extinction of *P. lanceolata*. Numbers on the contour lines indicate the probabilities of quasi-extinction. Darker shades of grey correspond with lower probabilities of quasi-extinction.

CONCLUSION

The research presented here addresses uncertainties posed by the New England Wildflower Society's conservation and research plan for *P. lanceolata* (Allard 2001) and the Massachusetts management plan for the species (Farnsworth *et al.* 2007). To conclude, I summarize the main results and provide some recommendations for the management of *P. lanceolata* based on the results of this research, so that it may be used to update the plans.

Although both plans for *P. lanceolata* identified non-native invasive species as a threat to the rare hemiparasite, there was no quantitative evidence that *P. lanceolata* in eastern populations where the species is considered as rare were more threatened by invasive species than populations in the Midwest where the species is considered as common. The data from the biogeographic study of in Chapter I showed that there were not different relative abundances of native, non-native invasive, non-native non-invasive, or species with both native and non-native genotypes associated with *P. lanceolata* in Eastern and Midwestern populations. This result suggests that of the sites sampled, *P. lanceolata* populations along the east coast are not at greater risk of interactions with non-native invasives than are populations in Midwest.

There was also no evidence that *P. lanceolata* preferred native over invasive hosts. The greenhouse study in Chapter II showed that *P. lanceolata* had higher growth rates, survival, and flowering when grown with the native hosts *Juncus effusus* and *Scirpus cyperinus* than when grown with the invasive hosts *B. inermis* and *P. arundinacea.* However, in the field removal experiment, the growth of *P. lanceolata* was not consistently greater from year to year in plots where non-natives were removed than

in plots where natives were removed. The inconsistency of the results for the field removal experiment may be due to succession of native woody shrubs at the site over the course of the study. These results suggest that the distinction between the effects of natives and invasives is not black and white. While *P. lanceolata* grow better with some natives compared to invasives, not all natives are ideal associated species. For instance, woody natives that can cause the transition of *P. lanceolata*'s preferred early successional habitat to mid-successional habitat may be as much of a threat to *P. lanceolata*'s persistence as invasive species.

The results of the stochastic population projections in Chapter III supported this notion. *Pedicularis lanceolata* growing in uninvaded patches had lower population growth rates than plants growing in invaded populations in the stochastic demographic models. The deterministic demographic models showed that the population growth rate in uninvaded patches was greater in 2007-2008 compared to invaded patches, but that in 2008-2009 the invaded patches had higher growth rates. This result coincides with the observation that native shrubs became more dominant at the site in 2008-2009.

This information suggests that the management of sites with *P. lanceolata* must focus not only on removing invasive species, but also on maintaining early successional habitat. The results of the field experiment in which plots with all plants removed had low survival and growth of *P. lanceolata* showed that the removal of woody vegetation and invasive species needs to be selective and not harm all host plants simultaneously. Further, the use of certain herbicides may be risky to *P. lanceolata* if it is possible for the

herbicides to travel from the host to the hemiparasite through the haustorial connection. For invasive species, the best management may be to prevent the invasion in the first place if possible.

The results of the metapopulation model for *P. lanceolata* in Chapter IV provide some additional insights into the challenge of managing *P. lanceolata* across multiple sites. In the simulation analysis, the probability of dispersal had to be high (~0.17) for effective metapopulation dynamics. Also, the probability of a catastrophic year had a significant effect on the probability of quasi-extinction of *P. lanceolata*. Given that it is difficult to predict catastrophic events, the establishment of additional sites with *P. lanceolata* would decrease the probability that the entire population would go extinct if many of the sites were devastated. The establishment of new sites could be accomplished in a number of ways. One option would be to increase and maintain the amount of suitable habitat patches along the brook where *P. lanceolata* grows by removing invasives and woody vegetation. Another option would be to directly establish new sites with *P. lanceolata* by planting out seeds or seedlings.

Although the data presented here answer some of the questions posed by the plans, there is still much more to learn about *P. lanceolata*. For instance, the establishment of new sites with *P. lanceolata* along the brook would require additional information on what sites might be most resilient to catastrophic events, such as beaver flooding. Also, the results of the metapopulation simulations show that additional information on the probability of catastrophes and the dynamics of beaver at the sites are crucial to assessing the extinction risk of the population. While this research provides information to adapt the management plan, the revision of the plan and management of

the species are ongoing processes. Further, the data presented here show that there are multiple threats to *P. lanceolata* (*e.g.*, beaver activity, succession, competition with invasive species), emphasizing the importance of being open-minded to the many factors that influence the persistence of endangered species when writing management plans and putting them into action in the field

APPENDIX I

2007-2009 ANNUAL REPORTS SUBMITTED BY S. RECORD TO THE MASSACHUSETTS NATURAL HERITAGE AND ENDANGERED SPECIES PROGRAM

2007 Report

Research Question 1 – *What invasives are associated with P. lanceolata?*
(See previously submitted research proposal and Management Plan for *P. lanceolata* (Farnsworth et al. 2007))

At the Massachusetts population I have not found any additional invasive species beyond those documented on previous field forms. Last summer in addition to the funding from the Massachusetts Natural Heritage Program to visit populations of *P. lanceolata* in Connecticut, I received travel awards from the University of Massachusetts Natural History Collections and Plant Biology Graduate Program to visit populations of the species in the midwestern and southeastern United States. I sampled 22 populations of *P. lanceolata*. Eleven core (midwestern) populations were in Wisconsin and Illinois. Eleven edge (eastern) populations were in Connecticut, New York, Tennessee, and North Carolina. I recorded associated plant species and their abundances in cover classes within half-meter and one-meter diameter circles centered on five focal *P. lanceolata* plants per population.

Pedicularis lanceolata co-occurred with over 280 plant species, 19 of which were invasive according to the United States Department of Agriculture's PLANTS Database (Table A1.1). The most frequently co-occurring invasives were *Phalaris arundinacea* (Reed Canarygrass) and *Rhamnus cathartica* (Glossy Buckthorn). The most frequently co-occurring native species were *Lycopus uniflorus* (Northern Bugleweed) and *Solidago* species (Goldenrods). Invasives species co-occurred with *P. lanceolata* in 16 of the 22 populations sampled (8 populations in the Midwest and 8 populations along the east coast). Core, midwestern populations versus edge, eastern populations differed significantly in species similarity (*t test* on average Simpson's Similarity Index Comparisons between versus within regions, $P = 0.59 \times 10^{-10}$) (Fig. A1.1). Midwestern and eastern populations did not, however, differ significantly in the proportion of invasive species present (*G test*, $P = 0.71$).

Research Question 2 - Do co-occurring invasives interact with *P. lanceolata* positively as facilitative host plants or negatively as competitors?

Last spring I proposed an experiment that would separate aboveground competitive effects of native and invasive host plants with *P. lanceolata* from belowground facilitative effects using an aboveground barrier treatment. At the advice of my dissertation committee, I decided to try an alternate cutting treatment instead of the aboveground barrier treatment. From mid-July to early October, I performed a pilot experiment with two treatments: 1) aboveground biomass of hosts clipped (facilitation

only) and 2) aboveground biomass of hosts not clipped (competition and facilitation). The objective of this pilot was to see if clipping the aboveground biomass of host plants would cause the plants to allocate more biomass to their roots, which would be an unwanted confounding variable for a full-scale experiment. The three host plant species in this experiment were *Juncus effusus*, *Phalaris arundinacea*, and *Scirpus cyperinus*. Plants were potted in single species arrays of one or three plants per pot. The total sample size was 68 pots (3 host species × 2 densities × 2 treatments × 6 replicates (with the exception of the *P. arundinacea* arrays with 3 plants, which only had 3 replicates per treatment) = 68 pots). In early October, I harvested the above- and belowground biomasses of all pots. I am in the process of sorting roots from soil and analyzing the data from this pilot experiment.

I tried to germinate seeds of *P. lanceolata* purchased from a commercial nursery in the Midwest using variations of Baskin and Baskin's protocol (Baskin and Baskin 2002). I sterilized seeds in a 20% bleach solution for 15 minutes then transferred to moistened filter paper in petri dishes under sterile conditions. Seeds within petri dishes were stored in a refrigerator to simulate cold, moist stratification for 2, 4, 6, or 8 weeks. There were 100 seeds per treatment. Following stratification, I potted seeds into loam in the greenhouse. None of the 400 seeds germinated. During the winter and spring I am going to experiment with gibberellic acid treatments to try to trick the seeds out of dormancy.

This fall I potted all of the host plants for a full-scale experiment. The four host species for the experiment are: the natives *Juncus effusus* and *Scirpus cyperinus* and the non-natives *Bromus inermis* and *Phalaris arundinacea*. All of these host plants are or have been associated with *P. lanceolata* along Broad Brook according to personal observations and field forms. I potted host plants in single species arrays of one, two, or three plants per pot. There will be two treatments: competition only and competition and facilitation. Contingent upon the results of the pilot experiment, I will or will not implement the clipping or no clipping treatments in this full-scale experiment. The total sample size is 240 pots (4 host species × 3 densities × 2 treatments × 10 replicates = 240 pots). Pots with host densities of one or two plants will have respectively either two or one *P. lanceolata* individuals planted into them through fall sowing of seeds or spring planting of seedlings depending on germination success.

***Research Question 3* - How do *P. lanceolata* and other native plants respond to removal of invasives and encroaching woody vegetation?**

Subpopulation 5 Removal Experiment

four treatments for this field experiment: 1) an invasive species removal treatment 2) a native species removal treatment 3) an untreated control treatment and 4) a complete removal treatment in which all plants, both invasive and native, will be removed. Removals will consist of cutting and removing target plants.

Subpopulation 4 Phalaris Removal

On June 11, 2007 *Phalaris arundinacea* was cut using a weedwhacker from a 10m × 10m area surrounding subpopulation 4 with assistance from Walt Tyning and Kevin Pelowsky from the Massachusetts Division of Fisheries and Wildlife Belchertown office. Prior to the removal, stems of all plants and light measurements above and below the *P. arundinacea* canopy were recorded in both the 10m × 10m removal plot and an adjacent 10m × 10m control plot at twenty random 0.5m × 0.5m sample quadrats per

plot. The cutting was not selective and also removed some *Frangula alnus* and *Rosa multiflora*. We collected cut stems with rakes, put them into garbage bags, and placed the garbage bags in the field upland and to the east of the brook. Vegetation from the control and removal plots was re-sampled later in the growing season on August 16, 2007. The data did not meet the assumptions of a parametric one-way ANOVA test, so they were analyzed using the non-parametric Kruskal-Wallis test.

The removal was not very successful. There was no significance difference between the densities of *Phalaris arundinacea* stems before versus after the removal (Kruskal-Wallis test statistic $\chi_2^2 = 5.8111$, $P = 0.01593$). The density of non-*Phalaris* stems also did not differ before and after the removal ($\chi_2^2 = 2.2961$, $P = 0.1297$). Further, I only found seven ramets of *P. lanceolata* in the vicinity of subpopulation 4 in 2007. These individuals were not submerged under water and upland from the dense stand of *Phalaris* where the removal took place.

***Research Question 4* - What are the population trajectories and metapopulation dynamics of New England populations of *P. lanceolata*?**

Demographic Study

In the late summer and early fall, I tagged and mapped the locations of 1642 ramets of *P. lanceolata* along the brook (Table A1.2). I tagged plants with either plastic bird bands around their stems or aluminum tags staked into the ground next to them. I also set up a grid with rebar stakes hammered flush into the ground as corner markers every other meter and recorded the x- and y-coordinates of each ramet. For each ramet, I recorded the stem length, number of inflorescences, number of fruiting capsules, and number of leaves >6cm and ≤6cm in length. I recorded the area of all leaves for thirty of the ramets representing the range of stem lengths. I plan to use regression to create a predictive equation relating the leaf measurements that I took on all ramets to overall plant size based on a method employed on *Pedicularis furbishiae* by Gawler et al. (Gawler et al. 1987).

In November, I collected all of the capsules from 15 ramets in subpopulation 5 before their seeds dehisced. I took these capsules to the lab at Harvard Forest and quantified the number of seeds per capsule, viability of seeds, and signs of herbivory and mold. I returned all seeds to the base of their parent plants. On average there were 20 seeds per capsule, and the number of capsules per ramet ranged from 0 to 161. Of the 1841 seeds collected, 56% had little or no endosperm and did not appear viable. Fifty percent of the capsules collected showed signs of insect herbivory, and 74% of the capsules were moldy. I inadvertently collected a few of the larval seed predators, and I have a specimen fixed in ethanol that I am trying to identify.

Despite intensive searching, I was unable to relocate plants at subpopulations 1, 3, 6, and the newest subpopulation noted downstream and north of subpopulation 5 by Dave Fuller in the winter of 2006 (Table A1.2). Subpopulation 5 had the most plants (1415 ramets), but many of them were fragile seedlings. All subpopulations upstream and South of Subpopulation 5 experienced flooding from beaver activity. Most of subpopulation 4 was completely underwater for the entire growing season. Subpopulation 4 was much smaller than in previous years (7 ramets in 2007 versus 113 in 2006). The seven ramets found near subpopulation 4 this year were upland and not submerged by the beaver flooding. Subpopulations 1, 2, and 3 were not submerged until mid-August. The high amount of flowering ramets at subpopulation 2 might have been a stress response as

water inundated the plants as they were beginning to flower. Although there was a high proportion of flowering ramets at subpopulation 2, only six ramets produced fruits because many of the flowers mildewed before forming seed capsules. The preliminary demographic results from this year suggest that beaver activity exerts a strong impact on the dynamics of the subpopulations along the brook

Seedbank Study

To explore the seedbank dynamics of *P. lanceolata*, I sampled two soil cores every 50m along Broad Brook for 50m upstream and 50m downstream from all known subpopulations. In areas 50m up- or downstream from a known subpopulation, I took cores every 10m. A sub-sample of each core was planted into flats in the greenhouse, and I recorded the number of all species that germinated during the growing season. No *P. lanceolata* germinated from any of the soil cores. A second sub-sample of each core was sieved with running water then allowed to air dry. Over the winter, I will examine these sieved samples under a microscope to look for *P. lanceolata* seed.

2008 Report

Greenhouse Experiment

In the spring of 2008, none of the seed in the pots for the greenhouse experiment germinated. As a back-up, I also had sown into separate flats seeds that had been either moist cold-stratified, treated with varying concentrations of gibberellic acid (500 ppm, 1000ppm, 2000ppm), scarified, or a combination of the treatments. The seed supply was from Prairie Moon Nursery, a commercial nursery in Minnesota. The commercial seed was likely inviable given that none of the roughly 2,000 seeds that I planted germinated.

In June, I went to Ann Arbor, Michigan where *P. lanceolata* is not listed as a species of conservation concern and collected seedlings from several populations along the Huron River on land owned by the city of Ann Arbor's Metroparks. I transported these seedlings back to Massachusetts being careful not to inadvertently disperse any collected material en route. Mortality of transplanted seedlings into the pots for the greenhouse experiment was high, and I re-planted seedlings up until the end of August. There were not enough seedlings to follow through with the original experimental design where some pots were to have two *P. lanceolata* and one host plant, so we altered the design of the experiment to consist only of pots with a single *P. lanceolata* and two host plants. The design includes all possible combinations of the four host species in densities of two hosts grown with one *P. lanceolata* (Table 2.1).

Since seedlings were planted up until August, I delayed the originally scheduled first harvest of the plants in the fall of 2008 until June 2009. Harvesting the plants just one month after transplanting some of the seedlings was undesirable because it would likely have captured the influence of seedling vigor more than the effects of the clipping treatments. As such, we did not hire a work-study student this past fall. In June and September of 2009, all plants will be harvested, dried, and weighed to determine root versus shoot biomass of all species. We will hire a student this summer and use the funds from this research contract before the contract's June 30, 2009 end date for the first harvest.

Ideally, the full-scale design will consist of 240 pots (10 species arrays × 2 treatments × 2 harvests × 6 replicates). The number of replicates per treatment is high in case some of the *P. lanceolata* seedlings do not survive the winter of 2008-2009. In the spring of 2009, the final sample size will be determined based on *P. lanceolata* seedlings survivorship to maintain a balanced experimental design.

Field Removal Experiment

A Harvard Forest Summer Research Experiences for Undergraduates student and I maintained the clipping treatments for the field removal from early May 2008 until the end of September 2008. One confounding factor that I had not anticipated when planning the experiment was that since all of the plots were placed in highly invaded areas, the native removal plots would have much less biomass removed than the invasive removal plots. To address this, I dried and weighed all of the aboveground biomass removed from the clipping treatments throughout the summer to include biomass as a covariate when analyzing the experiment.

The preliminary results of the study show clear treatment effects despite unequal amounts of biomass removed from the plots (Fig. 2.2a). The clipping treatments significantly affected the percentage of change in the total stem length of *P. lanceolata* from 2007 to 2008 (one-way ANOVA $df = 8$, $F = 12.75$, $P = 0.002$). Removing non-native plants increased the percentage of change in the total stem length of *P. lanceolata* by nearly 400%.

The field removal treatments will continue for one more growing season in 2009. Other response variables measured in addition to stem length are seed output, seedling recruitment, and percentage of herbivory of the *P. lanceolata* in the central 0.5 m × 0.5 m of each plot. In the final analysis on the two years of post-treatment data, I will also include two covariates: the total number of *P. lanceolata* and the number of seed capsules produced by reproductive *P. lanceolata* in each 1 m × 1 m plot. Data will be analyzed using a repeated measures model to test for the effects of treatments and covariates within and between plots over time. Since the first year of data do not meet the ANCOVA assumption of homogeneity of regression coefficients, the model will include mixed effects to specify slopes for each treatment.

Demographic Study

The Subpopulations

This year I continued to follow tagged plants in the Massachusetts population. Table A1.3 summarizes the status of plants tagged in 2007 and new plants found in 2008 within the four subpopulations. For each stem, I recorded its height, number of inflorescences, number of fruiting capsules, and number of leaves >6cm and ≤6cm in length. I recorded the area of all leaves for thirty of the stems representing the range of heights. The field forms include detailed maps with information on the plots and subplots referenced in the demographic data Excel file. There is also a GIS layer of the plots in the zip filed entitled, "Pedlan_subpops.zip." This winter I am building the demographic model based on this first year of transition survival data. I was once again unable to find plants at subpopulations 1, 3, and 7 despite extensive searching. These subpopulations consisted of single to few plants and were all submerged under 1-2 feet of water as a result of beaver activity in 2007.

On a subset of flowering stems from subpopulation 5, I also recorded the number of seeds per fruiting capsule noting seed viability and sources of seed mortality, such as herbivory and mold. The average number of seeds set per fruiting capsule in 2008 was 18 seeds compared to 20 seeds in 2007. Sixty-two percent of capsules were moldy, and 62% of capsules showed signs of insect herbivory.

Field Germination Experiment

To quantify field germination rates of seeds, I used some of the seeds collected for examination in the lab in a germination experiment at the subpopulation 5 field site. There were two treatments in the experiment to determine the extent of seed predation by small mammals and other animals. In one treatment, I scraped off the top layer of soil and placed 100 seeds on the ground. In the other treatment, 100 seeds were placed within mesh bags in rodent proof cages. These treatments were paired and set up along a moisture gradient from wet to dry (or floodplain to upland) within 6 m from known plants. The total sample size is 15 pairs (3 in the wet floodplain, 3 in the intermediate moisture shrubline, and 3 in the dry upland). In the spring of 2009, I will count the number of seeds germinated in each treatment. Any seedlings will be planted near the parent plants from which the seeds were originally collected in October 2008.

Recruitment

The *P. lanceolata* growing along the brook exhibits metapopulation dynamics with separate subpopulations blinking in and out of existence along the brook over time. A key component in metapopulation modeling is to identify potential recruitment sites. For *P. lanceolata,* light availability is likely a limiting factor for recruitment. To determine the amount of and location of possible recruitment sites along the brook, a Harvard Forest summer REU student and I took spherical densiometer readings to measure canopy cover every 50 m along the brook. We took the readings at a height of 0.5 m (the average height of *P. lanceolata* stems). We covered approximately six kilometeres up- and downstream from the known subpopulations. We also measured the percent of canopy cover at the extant subpopulations in and near the known subpopulations.

Additional Plant Searches Along Broad Brook

While walking along the brook, we also kept an eye out for previously undocumented *P. lanceolata*. In areas with low canopy cover, we performed more extensive searches. A GIS layer for these additional search sites is in the zip file entitled, "2008_Pedlan_Search_Locations.zip." Unfortunately, we did not find any additional subpopulations.

Beaver Activity and Site History

While walking along the brook, we also quantified beaver activity by counting the number of stumps we saw (Fig. A1.4). Signs of beaver activity were highest in managed areas. Interestingly, the sites of highest beaver activity correspond to sites with low canopy cover and light conditions suitable for *P. lanceolata* to grow in. Site history is not included in this dissertation, but is archived at the Massachusetts Natural Heritage and Endangered Species Program office.

Stream Flow

I installed a pressure transducer to monitor flow conditions of the brook from October 2008 to May 2009. This information along with stream flow cross sections at times of low and high flow will also provide data on flood events that will be important when modeling seed dispersal in the metapopulation model.

2009 Report

Greenhouse Experiment

Methods

To compare *P. lanceolata* survival, growth, and haustoria production when grown with different host types and in the presence or absence of aboveground competition with these hosts, I conducted a factorial greenhouse experiment with three levels of host types (native, mixed and invasive) and two clipping treatments (clipped or unclipped hosts). Two native species (*Juncus effusus* L. and *Scirpus cyperinus* (L.) Kunth) and two invasive species (*Bromus inermis* Leyss. and *Phalaris arundinacea* L.) were used in the host arrays for the three levels of host type (Table 1).

Over-winter survival of *P. lanceolata* seedlings was recorded in May 2009. Pots in which *P. lanceolata* did not survive the winter were removed from the experiment at the end of May 2009. Half of the remaining pots were harvested in the third week of June 2009, and the other half of the remaining pots were harvested in the second week of August 2009. Two harvests were performed to document any phenological differences in haustoria formation. Before the August harvest, the number of inflorescences on each *P. lanceolata* was recorded. At this time, most of the reproductive *P. lanceolata* had produced buds and were flowering, but the flowering time of *P. lanceolata* in the field continues into September. Thus, the August flower measurements are conservative estimates of flower production. I hired a work-study student from UMass Amherst to assist with the harvests.

During each harvest, the above- and belowground plant material of each species was separated. Belowground material was separated from soil by spraying water on roots over a 0.25 mm sieve. Roots of the different species were separated based on differences in their color and morphology: *B. inermis* roots were pale yellow, *P. arundinacea* roots were whitish-pink with constrictions, *P. lanceolata* roots were stark white, *S. cyperinus* roots were brown and fibrous and *J. effusus* roots were dark red and fibrous. Haustoria on *P. lanceolata* and hosts were counted by examining hydrated belowground plant material under a dissecting microscope. Above- and belowground plant material was dried in an oven at 70°C for 72 hours until constant weight then weighed (±0.005 g).

A generalized linear model (glm) with a binomial error distribution (logit link) was used to to test for differences in the survival of *P. lanceolata* from the fall of 2008 to the spring of 2009. Categorical predictor variables used were clipping treatment, host type, and *P. lanceolata* source population; *P. lanceolata* initial size and transplant date were entered as a continuous covariate. A contingency table analysis was used to determine if winter mortality of *P. lanceolata* differed between treatments. Generalized linear models were also used to analyze the responses of *P. lanceolata* ln(total biomass) (Gaussian link), counts of the total number of haustoria per pot (Poisson link) and number of inflorescences produced at the second harvest (Poisson link). Categorical

predictor variables were clipping treatment, host type, harvest, and *P. lanceolata* source population; *P. lanceolata* initial size, transplant date, and total host biomass were continuous.

The primary objectives of this study were to determine the effects of host type, clipping, and a host type and clipping interaction on *P. lanceolata* performance. The interaction between host type and clipping was of interest from a management perspective where knowledge of how *P. lanceolata* performance might differ between host types and clipping treatments would provide guidance for removals or maintenance of hosts around sensitive populations of *P. lanceolata*. Given the objectives of the study and the large number of possible interaction terms for the glm models that could lead to increased family wise type I errors, for each glm all interactions except for the host type and clipping interaction were left out of the model because exclusion of the other interactions did not change the magnitudes of the effect sizes of the main effects (e.g., host type, clipping, *P. lanceolata* source, etc.) or host type and clipping interaction. Post-hoc pairwise comparisons among the three host types were carried out using Tukey's honest significant differences (HSD) test.

Table A1.1. A list of the invasive species associated with the 22 populations of *P. lanceolata* sampled. Check marks indicate those invasive species present at populations of *P. lanceolata* in Connecticut.

Species	Present in CT
Alliaria petiolata	x
Berberis thunbergii	x
Celastrus orbiculatus	x
Cirsium arvense	
Cuscuta gronovii	
Ligustrum vulgare	
Lonicera japonica	x
Lonicera morrowii	
Lythrum salicaria	x
Microstegium vimineum	x
Phalaris arundinacea	x
Phragmites australis	x
Poa compressa	
Polygonum cuspidatum	
Rhamnus cathartica	x
Rosa multiflora	x
Solanum dulcamara	x
Sonchus arvensis	

Table A1.2. Demographic results for 2007 at the *Pedicularis lanceolata* MA 004 occurrence.

Subpopulation	**# of Ramets**	**# of Flowering Ramets**	**# of Fruiting Ramets**
1	0	0	0
2	213	111	6
3	0	0	0
4	7	4	4
5	1415	238	213
6	7	6	6
7	0	0	0
Total	*1642*	*359*	*229*

Table A1.3. Summary of the status of tagged genets in each subpopulation as of Autumn 2008. These numbers vary slightly from the number of plants reported in the 2007 report because in 2007 we reported ramets rather than genets. Also, the 2007 numbers did not include all seedlings.

Subpopulation	Tagged in 2007, Survived to 2008	Tagged in 2007, Dead in 2008	New in 2008	Reproductive in 2008
2	2	98	12	2
4	3	3	10	6
5	444	1512	780	340
6	1	0	0	1
Total	450	1613	802	349

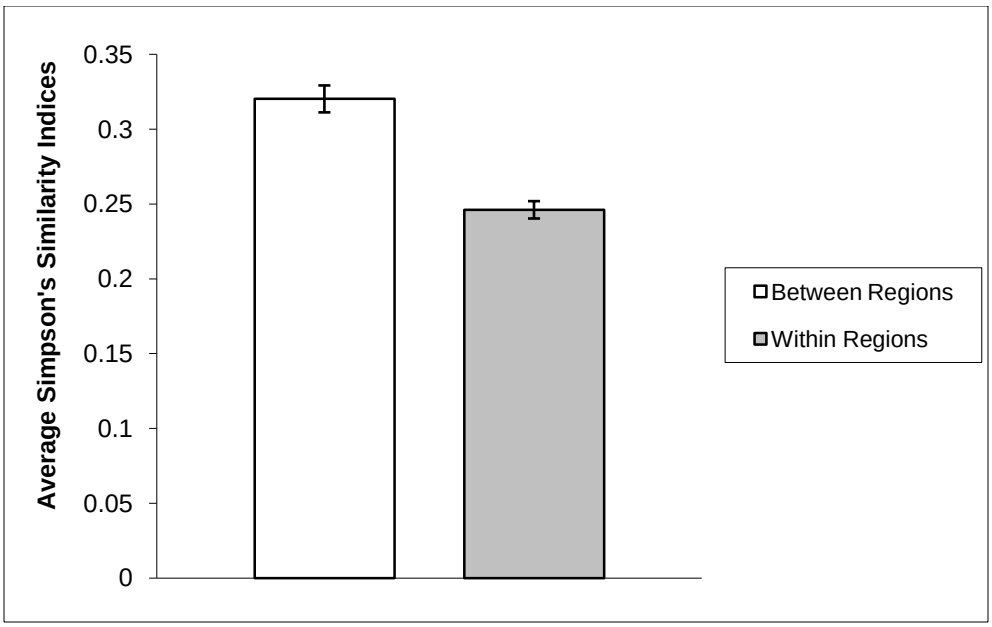

Figure A1.1. Core, midwestern and eastern, edge populations differed significantly in species similarity (*t* test, $P = 0.59 \times 10^{-10}$). Simpson's Similarity Index is a measure of β diversity ranging from 0 to 1 with a value of zero representing no common species between sites, and a value of one representing two sites having all of the same species.

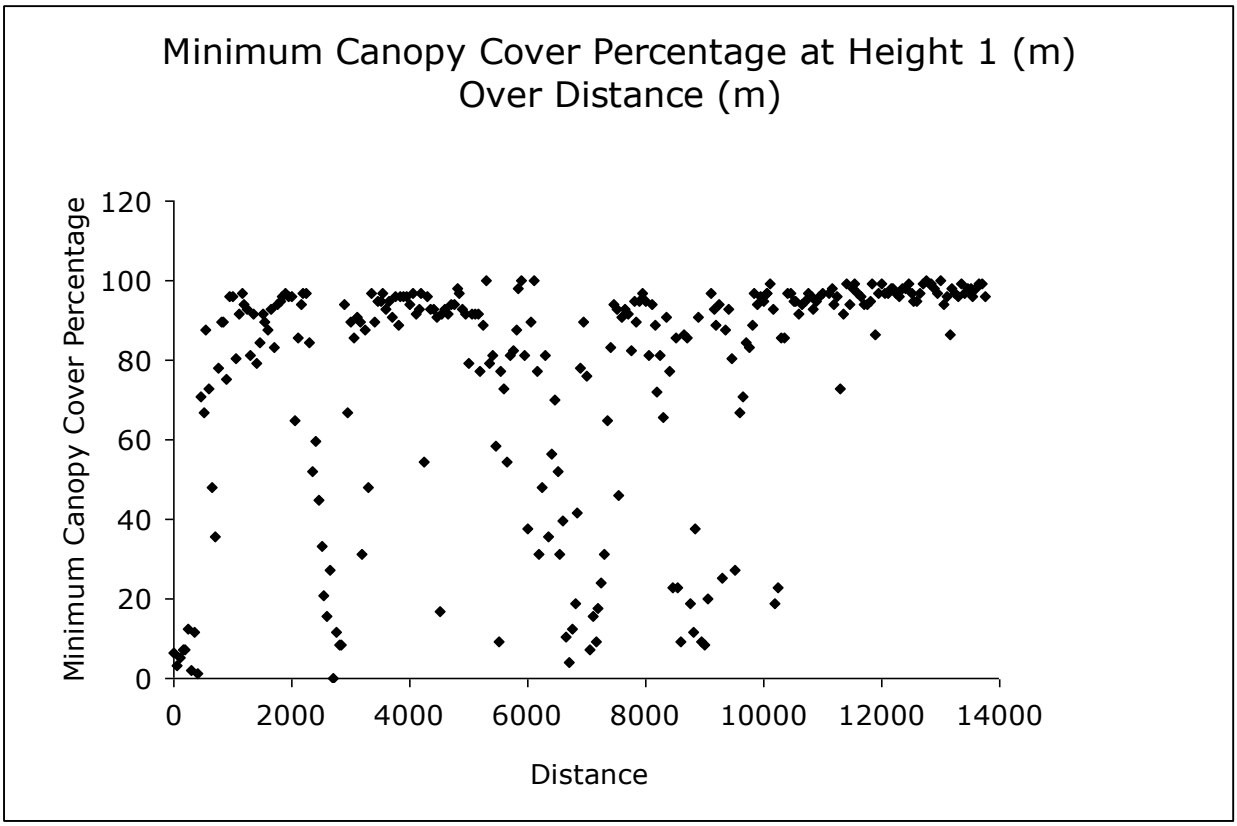

Figure A1.2. Percent canopy cover every 50 m along the brook.

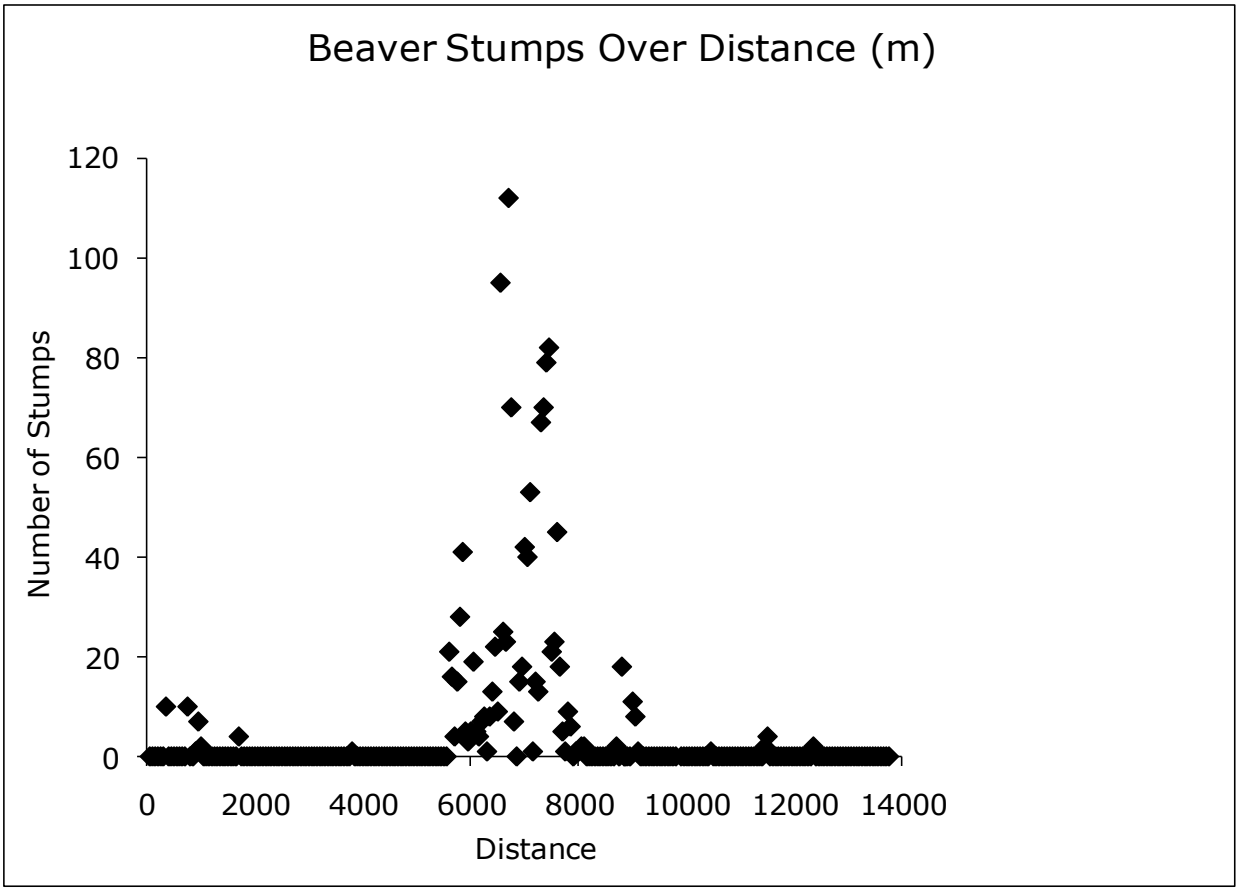

Figure A1.3. Number of beaver stumps found along the brook.

APPENDIX II

R CODE FOR CHAPTER THREE

```
# clear everything, just to be safe
rm(list=ls(all=TRUE))

# Load required packages
require(MCMCpack)

# Load data
setwd("specify working directory here")
data <- data.frame(read.csv("Data/subpop_5_LTRE.csv",header=TRUE))
year1.data <- subset(data, Year==0)
year2.data <- subset(data, Year==1)

# Determine max sizes of plants in each year
max(year1.data$t1_tot_lvs)
max(year2.data$t1_tot_lvs)
#=============================================================
#         Fit survering probability logistic regression
#=============================================================
# Prep data
adult.data <- subset(data, t1_new==0)
fl.i <- subset(adult.data, Inv_presence==1)
fl.n <- subset(adult.data, Inv_presence==0)

# Test for year effects
summary(glm(t0_flowering ~ log(t0_tot_lvs) + Year +
log(t0_tot_lvs)*Year,data=recruits, family="binomial"))

# There are year effects, so separate data by year.
fl.i.08 <- subset(fl.i, Year==0)
fl.i.09 <- subset(fl.i, Year==1)
fl.n.08 <- subset(fl.n, Year==0)
fl.n.09 <- subset(fl.n, Year==1)

# Fit Bayesian glms
# Code for weakly informative Cauchy prior.  t1_tot_lvs need to be centered to have
# mean = 0 and sd = 0.5.  Subtract mean from values and
# Center data on t1_tot_lvs
fl.i.08c <- log(fl.i.08$t1_tot_lvs)-mean(log(fl.i.08$t1_tot_lvs))
fl.i.08c <- fl.i.08c*(.5/sd(fl.i.08c))
fl.i.09c <- log(fl.i.09$t1_tot_lvs)-mean(log(fl.i.09$t1_tot_lvs))
fl.i.09c <- fl.i.09c*(.5/sd(fl.i.09c))
```

```
fl.n.08c <- log(fl.n.08$t1_tot_lvs)-mean(log(fl.n.08$t1_tot_lvs))
fl.n.08c <- fl.n.08c*(.5/sd(fl.n.08c))
fl.n.09c <- log(fl.n.09$t1_tot_lvs)-mean(log(fl.n.09$t1_tot_lvs))
fl.n.09c <- fl.n.09c*(.5/sd(fl.n.09c))

# Weakly informative prior function
logpriorfun <- function(beta, location, scale){
sum(dcauchy(beta, location, scale, log=TRUE))
}
set.seed(101)
fit.flowi08 <- MCMClogit(t0_flowering~fl.i.08c,data=fl.i.08,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52400
plot(fit.flowi08)
flow.alpha.i08 <- fit.flowi08[,1]
flow.beta.i08 <- fit.flowi08[,2]

set.seed(102)
fit.flowi09 <- MCMClogit(t0_flowering~fl.i.09c,data=fl.i.09,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52500
plot(fit.flowi09)
flow.alpha.i09 <- fit.flowi09[,1]
flow.beta.i09 <- fit.flowi09[,2]

set.seed(103)
fit.flown08 <- MCMClogit(t0_flowering~fl.n.08c,data=fl.n.08,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52145
plot(fit.flown08)
flow.alpha.n08 <- fit.flown08[,1]
flow.beta.n08 <- fit.flown08[,2]

set.seed(104)
fit.flown09 <- MCMClogit(t0_flowering~fl.n.09c,data=fl.n.09,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52782
plot(fit.flown09)
flow.alpha.n09 <- fit.flown09[,1]
flow.beta.n09 <- fit.flown09[,2]
```

```
#=============================================================
# Fit seedling size distribution, normal truncated at zero
#=============================================================
# Prep and load in data
recruit.data <- data.frame(read.csv("Data/subpop_5_LTRE_recruits.csv",header=TRUE))
recruits <- subset(data,t1_new==1)
hist(log(recruits$t1_tot_lvs)) # Graph it

# Test for year effects
summary(lm(log(t1_tot_lvs)~Year,data=recruits))
# Separate data by year
recruit.i08 <- subset(recruits, Inv_presence==1 & Year==0)
recruit.i09 <- subset(recruits, Inv_presence==1 & Year==1)
recruit.n08 <- subset(recruits, Inv_presence==0 & Year==0)
recruit.n09 <- subset(recruits, Inv_presence==0 & Year==1)
recruit.i <- subset(recruits, Inv_presence==1)
recruit.n <- subset(recruits, Inv_presence==0)
recruit.i.size <- recruit.i$t1_tot_lvs
recruit.n.size <- recruit.n$t1_tot_lvs
recruit.i08.size <- recruit.i08$t1_tot_lvs
recruit.i09.size <- recruit.i09$t1_tot_lvs
recruit.n08.size <- recruit.n08$t1_tot_lvs
recruit.n09.size <- recruit.n09$t1_tot_lvs
log.recruit.i08.size <- log(recruit.i08$t1_tot_lvs)
log.recruit.i09.size <- log(recruit.i09$t1_tot_lvs)
log.recruit.n08.size <- log(recruit.n08$t1_tot_lvs)
log.recruit.n09.size <- log(recruit.n09$t1_tot_lvs)

# Fit recruit size distribution
set.seed(105)
fit.log.recruit.i08 <- MCnormalnormal(log.recruit.i08.size,
        sigma2=var(recruit.i08.size),mu0=0,tau20=1000,mc=10000)
plot(fit.recruit.i08)
summary(fit.log.recruit.i08)
mean(fit.log.recruit.i08)

set.seed(106)
fit.log.recruit.i09 <- MCnormalnormal(log.recruit.i09.size,
        sigma2=var(recruit.i09.size),mu0=0,tau20=1000,mc=10000)
plot(fit.log.recruit.i09)
summary(fit.log.recruit.i09)
set.seed(107)
fit.log.recruit.n08 <- MCnormalnormal(log.recruit.n08.size,
        sigma2=var(recruit.n08.size),mu0=0,tau20=1000,mc=10000)
plot(fit.log.recruit.n08)
summary(fit.log.recruit.n08)
```

```
set.seed(108)
fit.log.recruit.n09 <- MCnormalnormal(log.recruit.n09.size,
        sigma2=var(recruit.n09.size),mu0=0,tau20=1000,mc=10000)
plot(fit.log.recruit.n09)
summary(fit.recruit.n09)


#============================================================
# Fit growth of surviving plants with linear model
#============================================================

# Test for year effects
summary(lm(log(t1_tot_lvs) ~ log(t0_tot_lvs)+Year+Year*log(t0_tot_lvs),data=growth))

# Separate data by year and invasiveness
growth.i08 <- subset(growth,Inv_presence==1 & Year==0)
plot(log(growth.i08$t0_tot_lvs),log(growth.i08$t1_tot_lvs))
growth.i09 <- subset(growth,Inv_presence==1 & Year==1)
plot(log(growth.i09$t0_tot_lvs),log(growth.i09$t1_tot_lvs))
growth.n08 <- subset(growth,Inv_presence==0 & Year==0)
plot(log(growth.n08$t0_tot_lvs),log(growth.n08$t1_tot_lvs))
growth.n09 <- subset(growth,Inv_presence==0 & Year==1)
plot(log(growth.n09$t0_tot_lvs),log(growth.n09$t1_tot_lvs))

# Fit regressions with x=size at time t and y=size at time t+1
set.seed(109)
fit.growth.i08 <- MCMCregress(log(t1_tot_lvs)~
        log(t0_tot_lvs),data=growth.i08,mc=10000)
plot(fit.growth.i08)
fit.growth.beta0.i08 <- fit.growth.i08[,1]
fit.growth.beta1.i08 <- fit.growth.i08[,2]
fit.growth.sigma2.i08 <- fit.growth.i08[,3]

set.seed(110)
fit.growth.i09 <- MCMCregress(log(t1_tot_lvs)~
        log(t0_tot_lvs),data=growth.i09,mc=10000)
#plot(fit.growth.i09)
fit.growth.beta0.i09 <- fit.growth.i09[,1]
fit.growth.beta1.i09 <- fit.growth.i09[,2]
fit.growth.sigma2.i09 <- fit.growth.i09[,3]

set.seed(111)
fit.growth.n08 <- MCMCregress(log(t1_tot_lvs)~
        log(t0_tot_lvs),data=growth.n08,mc=10000)
plot(fit.growth.n08)
```

```
fit.growth.beta0.n08 <- fit.growth.n08[,1]
fit.growth.beta1.n08 <- fit.growth.n08[,2]
fit.growth.sigma2.n08 <- fit.growth.n08[,3]

set.seed(112)
fit.growth.n09 <- MCMCregress(log(t1_tot_lvs)~
        log(t0_tot_lvs),data=growth.n09,mc=10000)
plot(fit.growth.n09)
fit.growth.beta0.n09 <- fit.growth.n09[,1]
fit.growth.beta1.n09 <- fit.growth.n09[,2]
fit.growth.sigma2.n09 <- fit.growth.n09[,3]
summary(fit.growth.n09)

#============================================================
# Fit seed production function: Poisson regression
#============================================================
# Fecundity (seed production)
# 19 seeds per capsule on average
library(gplots)
seed.producers <- subset(data,t1_caps==1)

# Test for year effects
summary(lm(no_seeds~llvs+Year+Year*llvs,data=seed.producers))

set.seed(301)
fit.seed.i.08pois <-MCMCpoisson(t1_no_seeds~lvs08i.centered,data=seed.i.08)
plot(fit.seed.i.08pois)
summary(fit.seed.i.08pois)
fit.seed.beta0.i08 <- fit.seed.i.08pois[,1]
fit.seed.beta1.i08 <- fit.seed.i.08pois[,2]
plot(lvs08i.centered,seed.i.08$t1_no_seeds)

set.seed(300)
fit.seed.i.09pois <-MCMCpoisson(t1_no_seeds~lvs09i.centered,data=seed.i.09)
plot(fit.seed.i.09pois)
summary(fit.seed.i.09pois)
plot(log(seed.i.09$t1_tot_lvs),seed.i.09$t1_no_seeds)
plot(lvs09i.centered,seed.i.09$t1_no_seeds)
fit.seed.beta0.i09 <- fit.seed.i.09pois[,1]
fit.seed.beta1.i09 <- fit.seed.i.09pois[,2]

set.seed(303)
fit.seed.n.08pois <-MCMCpoisson(t1_no_seeds~lvs08n.centered,data=seed.n.08)
plot(fit.seed.n.08pois)
summary(fit.seed.n.08pois)
plot(log(seed.n.08$t1_tot_lvs),(seed.n.08$t1_no_seeds))
```

```
plot(lvs08n.centered,seed.n.08$t1_no_seeds)
fit.seed.beta0.n08 <- fit.seed.n.08pois[,1]
fit.seed.beta1.n08 <- fit.seed.n.08pois[,2]

set.seed(302)
fit.seed.n.09pois <-MCMCpoisson(t1_no_seeds~lvs09n.centered,data=seed.n.09)
plot(fit.seed.n.09pois)
summary(fit.seed.n.09pois)
plot(log(seed.n.08$t1_tot_lvs),(seed.n.08$t1_no_seeds))
plot(lvs09n.centered,seed.n.09$t1_no_seeds)
fit.seed.beta0.n09 <- fit.seed.n.09pois[,1]
fit.seed.beta1.n09 <- fit.seed.n.09pois[,2]

#============================================================
# Fit survival with logistic regression
#============================================================

# Prep and load data
surv.data <- data.frame(read.csv("Data/surv_data.csv",header=TRUE))
surv.data.adults <- subset(surv.data, X08_new==0 & X09_new==0)

surv.datai.adults <- subset(surv.data.adults, Inv_presence==1)
surv.datan.adults <- subset(surv.data.adults, Inv_presence==0)

surv.data.i <- subset(surv.data, Inv_presence==1)
surv.data.i <- surv.data.i[,6:8]
surv.data.n <- subset(surv.data, Inv_presence==0)
surv.data.n <- surv.data.n[,6:8]

# Test for year effects
summary(glm(t1_presence ~ log(t0_tot_lvs) + Year + log(t0_tot_lvs)*Year,data=recruits,
family="binomial"))

# There are year effects, so separate data by year.
surv.data.i08 <- subset(surv.data, Inv_presence==1 & Year==0)
surv.data.i09 <- subset(surv.data, Inv_presence==1 & Year==1)
surv.data.n08 <- subset(surv.data, Inv_presence==0 & Year==0)
surv.data.n09 <- subset(surv.data, Inv_presence==0 & Year==1)

# Fit Bayesian glms
# Code for weakly informative Cauchy prior.  t1_tot_lvs need to be centered to have
# mean = 0 and sd = 0.5.  Subtract mean from values and

# Center data on t1_tot_lvs
surv.i.08c <- log(surv.i.08$t1_tot_lvs)-mean(log(surv.i.08$t1_tot_lvs))
surv.i.08c <- surv.i.08c*(.5/sd(surv.i.08c))
```

```
surv.i.09c <- log(surv.i.09$t1_tot_lvs)-mean(log(surv.i.09$t1_tot_lvs))
surv.i.09c <- surv.i.09c*(.5/sd(surv.i.09c))
surv.n.08c <- log(surv.n.08$t1_tot_lvs)-mean(log(surv.n.08$t1_tot_lvs))
surv.n.08c <- surv.n.08c*(.5/sd(surv.n.08c))
surv.n.09c <- log(surv.n.09$t1_tot_lvs)-mean(log(surv.n.09$t1_tot_lvs))
surv.n.09c <- surv.n.09c*(.5/sd(surv.n.09c))

# Weakly informative prior function
logpriorfun <- function(beta, location, scale){
sum(dcauchy(beta, location, scale, log=TRUE))
}

set.seed(101)
fit.survi08 <- MCMClogit(t0_survering~surv.i.08c,data=surv.i.08,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52400
plot(fit.survi08)
surv.alpha.i08 <- fit.survi08[,1]
surv.beta.i08 <- fit.survi08[,2]

set.seed(102)
fit.survi09 <- MCMClogit(t0_survering~surv.i.09c,data=surv.i.09,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52500
plot(fit.survi09)
surv.alpha.i09 <- fit.survi09[,1]
surv.beta.i09 <- fit.survi09[,2]

set.seed(103)
fit.survn08 <- MCMClogit(t0_survering~surv.n.08c,data=surv.n.08,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52145
plot(fit.survn08)
surv.alpha.n08 <- fit.survn08[,1]
surv.beta.n08 <- fit.survn08[,2]

set.seed(104)
fit.survn09 <- MCMClogit(t0_survering~surv.n.09c,data=surv.n.09,
        user.prior.density=logpriorfun,logfun=TRUE,location=0,
        scale=10,mc=10000) # acceptance rate 0.52782
plot(fit.survn09)
surv.alpha.n09 <- fit.survn09[,1]
surv.beta.n09 <- fit.survn09[,2]
#============================================================
# Function for the deterministic population growth rate (lambda)
```

```
# Insert posteriors (e.g., surv.alpha.i08) that correspond to treatment and year to be
#modeled. Here an invaded patch in 2008-2009 is modeled.
# Inputs:
# max.size = the maximum observed size
# bigM = the number of meshpoints in the approximating matrix
# iter = the number of iterations

# Outputs:
# A vector of lambda values that is the length of iter.
lambda.i08 <- function(max.size, bigM, iter){
                lambda <- vector('numeric',iter)
                for(i in 1:iter){
                        sx<-function(x) {
                        u<-exp(mean(surv.alpha.i08)+(mean(surv.beta.i08)*x))
                                return(u/(1+u))
                                }
                        gyx <-function(y,x) {
                    mux<-mean(fit.growth.beta0.i08)+(mean(fit.growth.beta1.i08)*x)
                                sigmax2<-mean(fit.growth.sigma2.i08)
                                sigmax<-sqrt(sigmax2)
                                fac1<-sqrt(2*pi)*sigmax
                                fac2<-((y-mux)^2)/(2*sigmax2)
                                return(exp(-fac2)/fac1)
                                }
                        pyx=function(y,x) {return(sx(x)*gyx(y,x))}
                        # Probability of flowering, logistic regression on size at
                        #time t+1
                        fx<-function(x) {
                       u<-exp(mean(flow.alpha.i08)+(mean(flow.beta.i08)*x))
                                return(u/(1+u));
                                }
                        fyx<-function(y,x) {
                                #expected number of seedlings after establishment
                     nseeds <- exp(mean(seed.alpha.i08)+(mean(seed.beta.i08)*x))
                                p.est <- p.est.i08
                                nkids<-p.est*nseeds
                                kidsize.mean<- recruit.mean.i08
                                kidsize.sd<- recruit.sd.i08
                                #probability of producing a seedling of size y
                                tmp<-dnorm(y,kidsize.mean,kidsize.sd)/(1-
                                        pnorm(0,kidsize.mean,kidsize.sd))
                                f<-fx(x)*nkids*tmp
                                return(f)
                                }
                        kyx=function(y,x) {pyx(y,x)+fyx(y,x)}
```

```
                        # Compute meshpoints iteration matrix KD
                        # Note the use of outer() to compute kernel values at all
                        #meshpoints in one statement.
                        h=log(max.size)/bigM
                        y=(h/2)*((0:(bigM-1))+(1:bigM));
                        K=outer(y,y,kyx);

                        KD=h*K;

                        # Get lamda from the iteration matrix, and plot
                        lambda[i]<- as.real(eigen(KD)$values[1])
                        }
        return(lambda=lambda)
}
#============================================================
# Function for the stochastic population growth rate (lambda)
# Insert posteriors (e.g., surv.alpha.i08) that correspond to treatment and year to be
modeled. Here the an invaded patch in 2008-2009 is modeled.
# Inputs:
# max.size = the maximum observed size
# bigM = the number of meshpoints in the approximating matrix
# iter = the number of iterations
# Outputs:
# A vector of lambda values that is the length of iter.

lambda.i08 <- function(max.size, bigM, iter){
        lambda <- vector('numeric',iter)
        for(i in 1:iter){
                sx<-function(x) {
            u<-exp(sample(surv.alpha.i08,1)+(sample(surv.beta.i08,1)*x))
                        return(u/(1+u))
                        }
                gyx <-function(y,x) {
                                        mux<-
    sample(fit.growth.beta0.i08,1)+(sample(fit.growth.beta1.i08,1)*x)
                        sigmax2<-sample(fit.growth.sigma2.i08,1)
                        sigmax<-sqrt(sigmax2)
                        fac1<-sqrt(2*pi)*sigmax
                        fac2<-((y-mux)^2)/(2*sigmax2)
                        return(exp(-fac2)/fac1)
                        }
                pyx=function(y,x) {return(sx(x)*gyx(y,x))}
                # Probability of flowering, logistic regression on size at
                #time t+1
                fx<-function(x) {
            u<-exp(sample(flow.alpha.i08,1)+(sample(flow.beta.i08,1)*x))
```

```
                                        return(u/(1+u));
                                        }
                                    fyx<-function(y,x) {
                                        #expected number of seedlings after establishment
            nseeds <- exp(sample(seed.alpha.i08,1)+(sample(seed.beta.i08,1)*x))
                                        p.est <- p.est.i08
                                        nkids<-p.est*nseeds
                                        kidsize.mean<- recruit.mean.i08
                                        kidsize.sd<- recruit.sd.i08
                                        #probability of producing a seedling of size y
        tmp<-dnorm(y,kidsize.mean,kidsize.sd)/(1-pnorm(0,kidsize.mean,kidsize.sd))
                                        f<-fx(x)*nkids*tmp
                                        return(f)
                                        }
                                    kyx=function(y,x) {pyx(y,x)+fyx(y,x)}

                                    # Compute meshpoints iteration matrix KD
                                    # Note the use of outer() to compute kernel values at all
                                    #meshpoints in one statement.
                                    h=log(max.size)/bigM
                                    y=(h/2)*((0:(bigM-1))+(1:bigM));
                                    K=outer(y,y,kyx);

                                    KD=h*K;

                                    # Get lamda from the iteration matrix, and plot
                                    lambda[i]<- as.real(eigen(KD)$values[1])
                                    }
                return(lambda=lambda)
}
#============================================================
# Function that calculates sensitivity and elasticity
# Insert posteriors (e.g., surv.alpha.i08) that correspond to treatment and year to be
modeled. Here the midpoint matrix for 2008-2009 is modeled.
# For the ad-hoc sensitivity and elasticity approach used for recruit size, all but one vital
rates' posterior(s) at a time would be set to the control (uninvaded)
# posteriors and one vital rate's posterior(s) would be set to the treatment (invaded). This
would be done in turn for each vital rate.
# Inputs:
# iter = the number of iterations
# Outputs:
# Three vectors of lambda, sensitivity, and elasticity values that are each of length iter.
set.seed(2000)
iterate.mid08.surv<- function(no.iter){
        sensitivity <- vector('numeric',no.iter)
        elasticity <- vector('numeric',no.iter)
```

```
lambda <- vector('numeric',no.iter)
for(i in 1:no.iter){
                    sx<-function(x) {
                        u<-exp((fit.survn.phi.mid)*x);
                        return(u/(1+u));
                        }
                    gxy <-function(x,y) {
        mux<-(fit.growth.beta0.mid08)+(fit.growth.beta1.mid08)*x
                        sigmax2<-(fit.growth.sigma2.mid08)
                        sigmax<-sqrt(sigmax2)
                        fac1<-sqrt(2*pi)*sigmax
                        fac2<-((y-mux)^2)/(2*sigmax2)
                        return(exp(-fac2)/fac1)
                        }
                    pyx=function(y,x) {return(sx(x)*gxy(x,y))}
                # Probability of flowering, logistic regression on size and age
                    fx<-function(x) {
                        u<-exp((flow.alpha.mid08)+(flow.beta.mid08)*x);
                        return(u/(1+u));
                        }
                    p.est <- 1
                    fyx<-function(y,x) {
                        #expected number of seedlings after establishment
                        nkids<-p.est
                        kidsize.mean<- (fit.recruit.mid08);
                        kidsize.var<- var(fit.recruit.i08)-var(fit.recruit.n08)
                        #probability of producing a seedling of size y
                tmp<-dnorm(y,kidsize.mean,sqrt(kidsize.var))/(1-
                    pnorm(0,kidsize.mean,sqrt(kidsize.var)))
                        f<-sx(x)*fx(x)*nkids*tmp;
                        return(f)
                        }
                    kyx=function(y,x) {pyx(y,x)+fyx(y,x)}
                    # Compute meshpoints iteration matrix KD
                # Note the use of outer() to compute kernel values at all
                #meshpoints in one statement.
                h=5/bigM; y=(h/2)*((0:(bigM-1))+(1:bigM));
                K=outer(y,y,kyx);
                KD=h*K;
                # Get lamda,v,w from the iteration matrix, and plot
                lambda[i]<- as.real(eigen(KD)$values[1])
                w.eigen=as.real(eigen(KD)$vectors[,1])
                w.eigen=w.eigen/sum(w.eigen);
                v.eigen=as.real(eigen(t(KD))$vectors[,1])
                v.eigen=v.eigen/v.eigen[1]
```

```
                    # Compute sensitivity and elasticity using sensitivity formulas
                    v.dot.w= h*sum(v.eigen*w.eigen)
                    # note <v,w> is an integral, done here by  midpoint rule.
                    sens.eigen=outer(v.eigen,w.eigen)/v.dot.w
                    sensitivity[i] <- mean(sens.eigen)
                    elas.eigen=K*sens.eigen/lambda[i]
                    elasticity[i] <- mean(elas.eigen)

                    }

        return(list(lambda=lambda, sensitivity=sensitivity, elasticity=elasticity))
        }
# End.
```

APPENDIX III

R CODE FOR CHAPTER FOUR

```
# Parameterize the metapopulation model

#clear everything, just to be safe
rm(list=ls(all=TRUE))

#Load required packages
require(nlme); require(MASS); require(glmmML)

# Parameterization for the vital rates of one patch.
# Each patch needs to be parameterized.

# Load data
setwd("specify working directory here")
data.5 <- data.frame(read.csv("Metapop_data/subpop_5_data.csv",header=TRUE))
surv.data.5 <- read.csv("Metapop_data/subpop5_surv_data.csv",header=TRUE)
surv.data.5 <- surv.data.5[,7:9]

#=================================================================
# Fit probability of producing seed capsules

# Test for year effects, yes there are
summary(glm(t1_flowering~log(t0_tot_lvs)+Year + log(t0_tot_lvs)*Year,
        family="binomial", data=fl.data.5))

# There are no year effects, so do not separate the data by year
n.fl.5 <- dim(fl.data.5)[1]
# Fit logistic regression model
fl5.glm <- glm(t0_caps~log(t0_tot_lvs), family="binomial", data=fl.data.5)
summary(fl5.glm)
fl5.beta0 <- fl5.glm$coefficients[1]
fl5.beta0.se <-  0.3497 # value from summary call
fl5.beta0.sd <- fl5.beta0.se*(sqrt(n.fl.5))
fl5.beta1 <- fl5.glm$coefficients[2]
fl5.beta1.se <-0.0986
fl5.beta1.sd <- fl5.beta1.se*(sqrt(n.fl.5))

#=================================================================
# Fit seedling size distibution, normal truncated at zero
recruits.5 <- subset(data.5, t1_new==1)
hist(recruits.5$t1_tot_lvs)
```

```
# Test for year effects
summary(lm(log(t1_tot_lvs)~Year,data=recruits.5))
# There are year effects, so separate the data by year:
recruits5.08 <- subset(recruits.5, Year==0)
n.recruits5.08 <- dim(recruits5.08)[1]

recruits5.09 <- subset(recruits.5, Year==1)
n.recruits5.09 <- dim(recruits5.09)[1]

# Parameterize 2008 data
lik<-function(p){
        lik<-sum(log(dnorm(log(recruits5.08$t1_tot_lvs),p[1],p[2])/(1-
pnorm(0,p[1],p[2]))))
return(-lik)
}
tmp<-optim(c(1,1),lik)
log.mean.size5.08<-tmp$par[1]
log.var.size5.08<-tmp$par[2]^2
sd.size5.08 <- sqrt(var.size5.08)

win.graph(); par(bty="l")
hist(recruits5.08$t1_tot_lvs,col="grey",xlab="Seedling size",main="")

s<-seq(0,30,length=100)
d<-dnorm(s,tmp$par[1],tmp$par[2])/(1-pnorm(0,tmp$par[1],tmp$par[2]))
diff<-s[2]-s[1]
lines(s,d*length(recruits5.08$t1_tot_lvs)/(2*sum(d*diff)))

# overplot normal distribution with same mean and variance
d<-dnorm(s,mean(recruits5.08$t1_tot_lvs),sd(recruits5.08$t1_tot_lvs))
lines(s,d*length(recruits5.08$t1_tot_lvs)/(2*sum(d*diff)),col="blue")

#Parameterize 2009 data
lik<-function(p){
        lik<-sum(log(dnorm(log(recruits5.09$t1_tot_lvs),p[1],p[2])/(1-
pnorm(0,p[1],p[2]))))
return(-lik)
}
tmp<-optim(c(0.5,0.5),lik) log.mean.size5.09<-tmp$par[1]
log.var.size5.09<-tmp$par[2]^2
sd.size5.09 <- sqrt(var.size5.09)

win.graph(); par(bty="l")
hist(recruits5.09$t1_tot_lvs,col="grey",xlab="Seedling size",main="")
```

```
s<-seq(0,30,length=100)
d<-dnorm(s,tmp$par[1],tmp$par[2])/(1-pnorm(0,tmp$par[1],tmp$par[2]))
diff<-s[2]-s[1]
lines(s,d*length(recruits5.09$t1_tot_lvs)/(2*sum(d*diff)))

# overplot normal distribution with same mean and variance
d<-dnorm(s,mean(recruits5.09$t1_tot_lvs),sd(recruits5.09$t1_tot_lvs))
lines(s,d*length(recruits5.09$t1_tot_lvs)/(2*sum(d*diff)),col="blue")

#============================================================
# Fit growth of plants from time t0 to time t1 using linear regression
# Graph data to see if linear model is appropriate or not
plot(growth.data.5$t1_tot_lvs~growth.data.5$t0_tot_lvs)
plot(log(data.5$t1_tot_lvs)~log(data.5$t0_tot_lvs), xlab="log(total leaves at t)"
        ylab="log(total leaves at t+1")
abline(a=growth5.beta0,b=growth5.beta1)
t1.lvs.5 <- subset(adult.data.5$t1_tot_lvs)
t0.lvs.5 <- log(adult.data.5$t0_tot_lvs)
year <- adult.data.5$Year

adult.data5.08 <- subset(adult.data.5, Year==0)
adult.data5.09 <- subset(adult.data.5, Year==1)

#Sample size
n.growth.5 <- dim(adult.data.5)[1]

# Test for year effects
summary(lm(log(t1_tot_lvs)~log(t0_tot_lvs)*Year +
log(t0_tot_lvs)*Year,data=adult.data.5))

# No year effects, so do not separate the data by year

# Fit linear model using gls
growth5.gls.year <- gls(log(t1_tot_lvs)~log(t0_tot_lvs) +
Year,weight=varExp(form=~fitted(.)),data=growth.data.5)
summary(growth5.gls.year)
growth5.gls <-
gls(log(t1_tot_lvs)~log(t0_tot_lvs),weight=varExp(form=~fitted(.)),data=growth.data.5)
summary(growth5.gls)
growth5.beta0 <- growth5.gls$coef[1]
growth5.beta0.se <- 0.10405551
growth5.beta0.sd <- growth5.beta0.se*(sqrt(n.growth.2))
growth5.beta1 <- growth5.gls$coef[2]
growth5.beta1.se <- 0.03425825
growth5.beta1.sd <- growth5.beta1.se*(sqrt(n.growth.2))
var.exp.5<-as.numeric(growth5.gls$modelStruct$varStruct[1])
```

```
sigma.5 <- growth5.gls$sigma
#============================================================
# Fit seed production with both negative binomial glm and poisson regression to see how
#results differ
# Select seed producing individuals from the data set
seed.producers.5 <- subset(grwot.data.5, t1_caps==1)

# Begin by plotting the data
plot(seed.producers.5$t1_no_seeds~seed.producers.5$t1_tot_lvs)
plot(seed.producers.5$t1_no_seeds~log(seed.producers.5$t1_tot_lvs))

#Check for year effects
#Negative binomial
year.glmnb <- (glm.nb(t1_no_seeds~t1_tot_lvs * factor(Year), data=seed.producers.5))
summary(year.glmnb)
logLik(year.glmnb)
AIC(year.glmnb)

#Poisson regression
year.pois <- glm(t1_no_seeds~t1_tot_lvs * factor(Year), data=seed.producers.5,
family="poisson")
summary(year.pois)
logLik(year.pois)
AIC(year.pois)

# Simple linear regression
year.lm <- lm(t1_no_seeds~t1_tot_lvs * factor(Year), data=seed.producers.5)
summary(year.lm)
logLik(year.lm)
AIC(year.lm)

# Separate data by year (there are year effects for the poisson regression, but not the
linear or glmnb models)
seed5.08 <- subset(seed.producers.5, Year==0)
dim(seed5.08)
seed5.09 <- subset(seed.producers.5, Year==1)
dim(seed5.09)

# Fit negative binomial glms
library(MASS)
seed5.glmnb <- glm.nb(t1_no_seeds~log(t1_tot_lvs), data=seed.producers.5)
summary(seed5.glmnb)
seed5.glmnb.beta0 <- summary(seed5.glmnb)$coefficients[1]
seed5.glmnb.beta0.se <- 0.0688339
seed5.glmnb.beta0.sd <- seed5.glmnb.beta0*(sqrt(seed5.08.glmnb.beta0.se))
seed5.glmnb.beta1 <- summary(seed5.glmnb)$coefficients[2]
```

```
seed5.glmnb.beta1.se <-0.0005373
seed5.glmnb.beta1.sd <- seed5.glmnb.beta1*(sqrt(seed5.08.glmnb.beta1.se))

seed5.08.glmnb <- glm.nb(t1_no_seeds~t1_tot_lvs, data=seed5.08)
summary(seed5.08.glmnb)
seed5.08.glmnb.beta0 <- summary(seed5.08.glmnb)$coefficients[1]
seed5.08.glmnb.beta0.se <- 0.1626790
seed5.08.glmnb.beta0.sd <- seed5.08.glmnb.beta0*(sqrt(seed5.08.glmnb.beta0.se))
seed5.08.glmnb.beta1 <- summary(seed5.08.glmnb)$coefficients[2]
seed5.08.glmnb.beta1.se <-0.0009278
seed5.08.glmnb.beta1.sd <- seed5.08.glmnb.beta1*(sqrt(seed5.08.glmnb.beta1.se))

seed5.09.glmnb <- glm.nb(t1_no_seeds~t1_tot_lvs, data=seed5.09)
summary(seed5.09.glmnb)
seed5.09.glmnb.beta0 <- summary(seed5.09.glmnb)$coefficients[1]
seed5.09.glmnb.beta0.se <- 0.0714380
seed5.09.glmnb.beta0.sd <- seed5.09.glmnb.beta0*(sqrt(seed5.09.glmnb.beta0.se))
seed5.09.glmnb.beta1 <- summary(seed5.09.glmnb)$coefficients[2]
seed5.09.glmnb.beta1.se <-0.0006346
seed5.09.glmnb.beta1.sd <- seed5.09.glmnb.beta1*(sqrt(seed5.09.glmnb.beta1.se))

# Fit poisson regressions
# No year effects followed by year effects
seed5.pois.year <- glm(t1_no_seeds~log(t1_tot_lvs)+Year, data=growth.data.5,
family="poisson")
summary(seed5.pois.year)

seed5.pois <- glm(t0_no_seeds~log(t0_tot_lvs), data=cap.data.5, family="poisson")
summary(seed5.pois)
seed5.pois.beta0 <- summary(seed5.pois)$coefficients[1]
seed5.pois.beta0.se <- 0.013137
seed5.pois.beta0.sd <- seed5.pois.beta0*(sqrt(seed5.pois.beta0.se))
seed5.pois.beta1 <- summary(seed5.pois)$coefficients[2]
seed5.pois.beta1.se <- 0.002812
seed5.pois.beta1.sd <- seed5.pois.beta1*(sqrt(seed5.pois.beta1.se))

seed5.08.pois <- glm(t1_no_seeds~t1_tot_lvs, data=seed5.08, family="poisson")
summary(seed5.08.pois)
seed5.08.pois.beta0 <- summary(seed5.08.pois)$coefficients[1]
seed5.08.pois.beta0.se <- 5.033e-03
seed5.08.pois.beta0.sd <- seed5.08.pois.beta0*(sqrt(seed5.08.pois.beta0.se))
seed5.08.pois.beta1 <- summary(seed5.08.pois)$coefficients[2]
seed5.08.pois.beta1.se <- 1.496e-05
seed5.08.pois.beta1.sd <- seed5.08.pois.beta1*(sqrt(seed5.08.pois.beta1.se))
```

```
seed5.09.pois <- glm(t1_no_seeds~t1_tot_lvs, data=seed5.09, family="poisson")
summary(seed5.09.pois)
seed5.09.pois.beta0 <- summary(seed5.09.pois)$coefficients[1]
seed5.09.pois.beta0.se <- 2.053e-03
seed5.09.pois.beta0.sd <- seed5.09.pois.beta0*(sqrt(seed5.09.pois.beta0.se))
seed5.09.pois.beta1 <- summary(seed5.09.pois)$coefficients[2]
seed5.09.pois.beta1.se <- 8.851e-06
seed5.09.pois.beta1.sd <- seed5.09.pois.beta1*(sqrt(seed5.09.pois.beta1.se))

# Fit linear models
seed5.08.lm <- lm(t1_no_seeds~t1_tot_lvs, data=seed5.08)
summary(seed5.08.lm)
seed5.08.lm.beta0 <- summary(seed5.08.lm)$coefficients[1]
seed5.08.lm.beta0.se <- 221.450
seed5.08.lm.beta1 <- summary(seed5.08.lm)$coefficients[2]
seed5.08.lm.beta1.se <- 1.264

seed5.09.lm <- lm(t1_no_seeds~t1_tot_lvs, data=seed5.09)
summary(seed5.09.lm)
seed5.09.lm.beta0 <- summary(seed5.09.lm)$coefficients[1]
seed5.09.lm.beta0.se <- 110.1633
seed5.09.lm.beta1 <- summary(seed5.09.lm)$coefficients[2]
seed5.09.lm.beta1.se <- 0.9791

# Graph it:
curve(exp(mean(seed5.09.pois.beta0)+mean(seed5.09.pois.beta1)*x),lwd=3, col="black",
lty=1,
        xlim=c(0,7),ylim=c(0,1000),cex.axis=1.2, cex.lab=1.2, ylab="Number of seeds
produced",
        xlab="Number of leaves at time t+1 (log scale)")
curve(exp(mean(seed5.08.pois.beta0)+mean(seed5.08.pois.beta1)*x),lwd=3,
col="darkgrey",  lty=1, add=TRUE)

# Poisson regression wins with AIC
#============================================================#
#Fit survival
# Select plants present at t0
surv.data.5 <- subset(data.5, t0_presence==1 & t1_new==0)

# Sample size
n.surv.data.5 <- dim(surv.data.5)[1]

# Test for year effects
surv5.year.glm <- glm(t1_presence~log(t0_tot_lvs)+Year + Year*log(t0_tot_lvs),
data=surv.data.5, family="binomial")
summary(aov(surv5.year.glm))
```

```
# There are no year effects, so keep data aggregated
# Fit logistic regression for survival
surv5.glm <- glm(t1_presence~log(t0_tot_lvs), data=surv.data.5, family="binomial")
summary(surv5.glm)
surv5.beta0 <- summary(surv5.glm)$coefficients[1]
surv5.beta0.se <- 0.3442
surv5.beta0.sd <- surv5.beta0.se*(sqrt(n.surv.data.5))
surv5.beta1 <- summary(surv5.glm)$coefficients[2]
surv5.beta1.se <-  .1208
surv5.beta1.sd <- surv5.beta1.se*(sqrt(n.surv.data.5))

#Separate year effects
surv.data.5.08 <- subset(surv.data.5, Year==0)
dim(surv.data.5.08)[1] #304
sum(surv.data.5.08$t1_presence)

surv.data.5.08.glm <- glm(t1_presence~log(t0_tot_lvs), data=surv.data.5.08,
family="binomial")
summary(surv.data.5.08.glm)

surv.data.5.09 <- subset(surv.data.5, Year==1)
dim(surv.data.5.09)[1] #411
sum(surv.data.5.09$t1_presence) #410
surv.data.5.09.glm <- glm(t1_presence~log(t0_tot_lvs), data=surv.data.5.09,
family="binomial")
summary(surv.data.5.09.glm)

#=============================================================
# Intra-specific density dependence analysis for recruitment
#=============================================================
# Plot the plot-level data
den.data <- read.csv("subpop5_data_dendep_20100605.csv", header=TRUE)

y.09 <- (den.data$Sum.of.New_09/(den.data$Sum.of.08_no_caps*19))
x.09 <- (den.data$Sum.of.08_no_caps*19)/den.data$Sum.of.08_prese
plot(y.09~x.09)

y.08 <- (den.data$Sum.of.New_08/(den.data$Sum.of.07_no_caps*19))
x.08 <- (den.data$Sum.of.07_no_caps*19)/den.data$Sum.of.07_presence

plot(y.08~x.08)
points(y.09~x.09, col="red")

predictor <- c(x.08,x.09)
response <- c(y.08,y.09)
```

```
response[response==Inf] <- NA
predictor[predictor==Inf] <- NA
response[is.nan(response)] <- NA
predictor[is.nan(predictor)] <- NA

not.these1 <- (1:length(response))[is.na(predictor)]
not.these2 <- (1:length(response))[is.na(response)]
response.short <- response[-c(not.these1,not.these2)]
predictor.short <- predictor[-c(not.these1,not.these2)]
plot(response.short~predictor.short)#,ylim=c(0,.05))


points(predictor.short,response.short,col='red')
nls1 <- nls(response.short ~ b*(1/predictor.short), start=c(b=1), trace=TRUE)
b<-summary(nls1)$parameters['b','Estimate']
curve(b*(1/x),add=TRUE, col='red')
b
x<-500
b/x
#=============================================================
# Metapopulation functions
#=============================================================
#  tmat.cor
#  This function incorporates spatial auto-correlation and positive correlation
#  in vital rates between sites.
#=============================================================
# Inputs:
#  no.subpops = the number of subpopulations to assign parameters to.
#  prob.pos.cor = the probability of positive correlation in vital rates between sites (i.e.,
#probability that #any local will be correlated with global)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each  #year and site for the three sites with more than one plant)
          #This is a vector giving the index numbers for each transition matrix (tmat).
#  prob.bad = the probability of an extreme event or 'bad' year (i.e., the probability that a
'bad' transition #matrix will be sampled)
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations
# Output:
#  subpop.tmat.sources = a vector specifying which transition matrices will be applied in
#year.step
```

```
tmat.cor <- function(
                        no.subpops,
                        prob.pos.cor=0,
                        no.tmats,
                        prob.bad= -1,
                        good.bad,
                        spatial.sd,
                        spatial.coef,
                        disp.dist.matrix
                    ){

          if(length(no.tmats) > 1){
                    if(prob.bad==-1){
                              prob.bad <- sum((good.bad=="bad")/length(good.bad))
                    }
                    weights <- vector('numeric', length(good.bad))
                    prob.good <- 1-prob.bad
                    weights.good <- prob.good/sum(good.bad=="good")
                    weights.bad <- prob.bad/sum(good.bad=="bad")
                    weights[good.bad=="good"] <- weights.good
                    weights[good.bad=="bad"] <- weights.bad

                    global.sample <- sample(x=no.tmats,1,replace=FALSE, prob=weights)

                    subpop.tmat.sources <- vector(mode='numeric', no.subpops)
        subpop.tmat.sources.good.bad <- vector(mode='character',length=no.subpops)
                    is.global <- rbinom(no.subpops,1,prob=prob.pos.cor)
                    for(i in 1:no.subpops){
                              if(is.global[i]==0){
         subpop.tmat.sources[i] <- sample(no.tmats,1,replace=FALSE,prob=weights)
                              }else{
                                        subpop.tmat.sources[i] <- global.sample
                              }

      subpop.tmat.sources.good.bad[i]<-good.bad[no.tmats==subpop.tmat.sources[i]][1]
                    }
                    subpop.tmat.sources.temp <- subpop.tmat.sources
                                        spatial.autocor.matrix <-
spatial.coef*(dnorm(disp.dist.matrix,mean=0,sd=spatial.sd)/dnorm(0,mean=0,sd=spatial.s
                                                  d))
                    kernel.order<-sample(1:no.subpops,no.subpops,replace=FALSE)
                    for(i in 1:no.subpops){
                              pop.num <- kernel.order[i]
```

```
   spatial.same <-rbinom(n=no.subpops,size=1,prob=spatial.autocor.matrix[,pop.num])
                        subpop.tmat.sources.temp[spatial.same==1]<-
subpop.tmat.sources[pop.num]

                }
                subpop.tmat.sources <- subpop.tmat.sources.temp

        }else{
                subpop.tmat.sources <- rep(no.tmats,no.subpops)
        }

        subpop.tmat.sources
}

#=============================================================#
tmat.sampler - builds a transition matrix
#=============================================================
# Inputs:
#  max.size = the maximum observed size of an individual in the population
#  bigM = the number of meshpoints in the iteration matrix (in the Pedicularis example
#bigM = 100)
#  tmat.subpop.sampler = specifies which subpopulation's transition matrix to use in
#calculating PD, #KIDD, and seeds(x).
#       In the year.step function tmat.subpop.sampler is the output of tmat.cor.
#  pvec.samples  = a list of the sampled estimates of the regressions for each vital rate
#(see #step.many.years() to see how estimation error is incorporated)
#  dd.p.est = Estimate resulting from nls model for intra-specific density dependence for
#recruitment.
# Output:
#  A list containing PD, KIDD, and seeds(x).
tmat.sampler <- function(
        max.size,
        bigM,
        tmat.subpop.sampler,
        pvec.samples,
        dd.p.est)
        {

                tmat.i <- tmat.subpop.sampler
                p.est <- dd.p.est
                                sx<-function(x) {
      u<-exp(pvec.samples[tmat.i,'surv.beta0'] + pvec.samples[tmat.i,'surv.beta1']*x)
                                        return(u/(1+u))
                                        }
                                gyx <-function(y,x) {
```

```
mux<- pvec.samples[tmat.i,'growth.beta0'] + pvec.samples[tmat.i,'growth.beta1']*x
                                        sigmax2<-
pvec.samples[tmat.i,'growth.sigma']*exp(2*pvec.samples[tmat.i,'growth.var.exp']*mux)
                                        sigmax<-sqrt(sigmax2)
                                        fac1<-sqrt(2*pi)*sigmax;
                                        fac2<-((y-mux)^2)/(2*sigmax2)
                                        return(exp(-fac2)/fac1)
                                        }
                                pyx=function(y,x) {return(sx(x)*gyx(y,x))}

                                fx<-function(x) {
        u<-exp(pvec.samples[tmat.i,'fl.beta0'] + pvec.samples[tmat.i,'fl.beta1']*x)
                                        return(u/(1+u))
                                        }

                                seedsx<-function(x) {
 nseeds <- exp(pvec.samples[tmat.i,'seed.beta0'] + pvec.samples[tmat.i,'seed.beta1']*x)
                                        num.seeds<-fx(x)*nseeds
                                        return(num.seeds)
                                        }
                                kidsy <- function(y){
                                        kidsize.mean<- pvec.samples[tmat.i,'recruit.mean']
                                        kidsize.var<- pvec.samples[tmat.i,'recruit.var']
                                        #probability of producing a seedling of size y
                        tmp<-dnorm(y,kidsize.mean,sqrt(kidsize.var))/(1-
                            pnorm(0,kidsize.mean,sqrt(kidsize.var)))
                                        kids<-p.est*tmp
                                        return(kids)
                                        }
                                # Compute meshpoints iteration matrix KD
                                # Note the use of outer() to compute kernel values at all
                                #meshpoints in one statement.
                                h=max.size/bigM
                                y=(h/2)*((0:(bigM-1))+(1:bigM));
                                P=outer(y,y,pyx)
                                PD=h*P
                                KID <- kidsy(y)
                                KIDD <- KID*h #sum(KIDD)==p.est
                                return(list(PD=PD,seedsx=seedsx,KIDD=KIDD))
                }
#============================================================
# year.step
#       This function iterates the model on time step and requires the tmat.cor
#       and tmat.sampler functions.
#============================================================
```

```
# Inputs:
#  Nt0 = a vector representing the initial size distribution. The length of this vector should
#equal bigM.
#  Seeds0 = a vector containing the initial number of seeds produced by each site. The
#length of this #vector should
#         equal the number of sites.
#  disp.prob.mat = a site x site dispersal probability matrix
#  pvec.samples  = a list of the sampled estimates of the regressions for each vital rate
#(see step.many.years() to see how estimation error is incorporated)
#  max.size = the maximum observed size of an individual in the population
#  no.subpops = the number of sites (or subpopulations)
#  prob.pos.cor = the probability of positive correlation (a value between 0 and 1)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each #year and site for the three sites with more than one plant)
#  prob.bad = the probability of a catastrophe or 'bad' year (a value between 0 and 1)
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations#
#
# Output:
#  A list containing Nt1 (a vector of length(bigM) for the size distribution for plants in the
#population at #time t+1), Seeds1 (a vector of length(no.subpops) containing
#         the number of seeds produced by each site at time t+1, and subpop.tmats (a vector
#of length(no.subpops) showing which transition matrix was selected for each site
#         (this is useful for error checking).

year.step <- function(Nt0,
                      Seeds0,
                      disp.prob.mat,
                      no.subpops,
                      max.size,
                      bigM,
                      prob.pos.cor,
                      no.tmats,
                      pvec.samples,
                      prob.bad,
                      good.bad,
                      spatial.sd,
                      spatial.coef,
                      disp.dist.matrix,
                      )
        {
```

```
PD.array <- array(NA,dim=c(no.subpops, bigM, bigM)) #PD is the growth/survival
                                        transition matrix
                        f <- matrix(NA,nrow=no.subpops,ncol=bigM)
                         #f is the new individuals arisen through dispersed fecundity
                        p <-  matrix(NA,nrow=no.subpops,ncol=bigM)
                         #p is the individuals arisen through growth/survival
      sum.seeds <- vector(mode='numeric', no.subpops)
      #number of seeds each population creates
      Nt1 <- matrix(NA,nrow=no.subpops,ncol=bigM) #next year's pop size
      h=max.size/bigM
      y=(h/2)*((0:(bigM-1))+(1:bigM))

                                subpop.tmats <- tmat.cor(
                                                        no.subpops=no.subpops,
                                                        prob.pos.cor=prob.pos.cor,
                                                        no.tmats=no.tmats,
                                                        prob.bad=prob.bad,
                                                        good.bad=good.bad,
                                                        spatial.sd=spatial.sd,
                                                        spatial.coef=spatial.coef,
                                                        disp.dist.matrix=disp.dist.matrix)
            dispersed.seeds <- matrix(NA,nrow=no.subpops,ncol=no.subpops)
                                dd.p.est <- vector('numeric', no.subpops)
                                for(i in 1:no.subpops){
                                        if( (sum(Nt0[i,])<0.5) & (Seeds0[i] < 1 ) ){
                                                Nt1[i,] <- 0
                                                dispersed.seeds[,i] <- 0
                                        }else{
dd.p.est.temp <- get.dd.p.est(number.of.seeds = Seeds0[i], number.of.plants sum(Nt0[i,]))
                dd.p.est[i] <- dd.p.est.temp * pvec.samples[subpop.tmats[i],'p.est']

tmat.temp <- tmat.sampler(max.size=max.size, bigM=bigM,
tmat.subpop.sampler=subpop.tmats[i],
pvec.samples=pvec.samples, dd.p.est=dd.p.est[i])
                                                }
                                                f[i,] <- Seeds0[i]*tmat.temp$KIDD

                                                PD.array[i,,] <- tmat.temp$PD

                                                p[i,] <- Nt0[i,]%*%PD.array[i,,]
                                                seeds.temp <- tmat.temp$seedsx(y)*Nt0[i,]
                                                sum.seeds[i] <- round(sum(seeds.temp*h))
                                    dispersed.seeds[,i] <- disp.prob.mat[,i]*sum.seeds[i]
                                                Nt1[i,] <- f[i,] + p[i,]
                                        }
                                }
```

```
                        Seeds1 <- apply(dispersed.seeds,1,sum)
                        #this is the number of new seeds arriving at each
                        #population at the end of the time step
                                K=50000
                        #       max of 112 plants/meter
                        #       patches are 50x10m = 500
                        #       max plants are 56,000 = 500*112
                                for(i in 1:no.subpops){
                                        if( sum(Nt1[i,]) > K){
                                                Nt1[i,] <- Nt1[i,] / (sum(Nt1[i,])/K)
                                        }
                                }

        return(list(Nt1=Nt1,Seeds1=Seeds1,subpop.tmats=subpop.tmats))
        }
#=============================================================
 # Function to get density dependent p.est during iterations with multiple years (required
by step.many.years function)
#=============================================================
get.dd.p.est <- function(number.of.seeds,number.of.plants){
                        predictor <- number.of.seeds/number.of.plants
                        if( predictor < 149){
                                dd.p.est  <- max(pvec$p.est)
                        }else{
                                dd.p.est <- 2.97 / predictor
                        }
                        return(dd.p.est)
                }

#=============================================================
# step.many.years
#       Iterates the model multiple years. This function requires these functions:
#year.step, tmat.sampler, get.dd.p.est,
#       and tmat.cor.Estimation error is sampled in step.many.years()
#       by sampling from distributions for the regression coefficients of the vital rates at
#the beginning of each 50 year run
#     followed by the calculation of PD, KIDD, and seeds(x).
#=============================================================
# Inputs:
#  no.years = number of years to iterate the model
#  Nt0 = a vector representing the initial size distribution. The length of this vector should
#equal bigM.
#  Seeds0 = a vector containing the initial number of seeds produced by each site. The
#length of this #vector should
#       equal the number of sites.
#  disp.prob.mat = a site x site dispersal probability matrix
```

```
#  pvec = a list of the estimates of the regressions for each vital rate
#  max.size = the maximum observed size of an individual in the population
#  bigM = the number of meshpoints in the iteration matrix (in the Pedicularis example
#bigM = 100)
#  no.subpops = the number of sites (or subpopulations)
#  prob.pos.cor = the probability of positive correlation (a value between 0 and 1)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each #year and site for the three sites with more than one plant)
#  prob.bad = the probability of a catastrophe or 'bad' year (a value between 0 and 1)
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations
#
# Output:
#  Returns a vector, Nt.sum, of length(no.years), which is the number of individuals in the
#population at each time step.

step.many.years <- function(
        no.years,
        Nt0,
        Seeds0,
        disp.prob.mat,
        no.subpops,
        pvec,
        max.size,
        bigM,
        prob.pos.cor,
        no.tmats,#number of observed transition matrices
        prob.bad,
        good.bad,
        spatial.sd,
        spatial.coef,
        disp.dist.matrix)
        {

        plot(0,sum(Nt0),xlim=c(0,50),ylim=c(0,(10*(sum(Nt0)))),xlab="Year",
                ylab="Number of Plants")
        abline(h=100)
        Nts <- array(NA, dim=c(no.subpops,bigM,no.years))
        Nts[,,1] <- Nt0
        Seedss <- matrix(NA,nrow=no.subpops,ncol=no.years)
        Seedss[,1] <- Seeds0
```

```
Nts.sum <- vector('numeric',no.years)
Nts.sum[1] <- sum(Nt0)

#in each 50-year iteration:
var.names <- c('surv.beta0','surv.beta1','growth.beta0','growth.beta1','growth.sigma',
'growth.var.exp','fl.beta0','fl.beta1','seed.beta0','seed.beta1','recruit.mean',
'recruit.var','p.est')
pvec.samples <- matrix(data=NA, nrow=length(no.tmats), ncol=length(var.names),
dimnames = list(NULL,var.names))
# nrow is the number of observed transitions (in this case 6 observed + 1
#intermediate from averaged good and bad extremes)
# ncol = number of vital rate parameters
#to adjust density dependent p.est
p.est.mean <- mean( pvec$p.est )

for(i in 1:length(no.tmats)){
tmat.i <- i
pvec.samples[i,'surv.beta0'] <- rnorm(1, pvec$surv.beta0[tmat.i],
pvec$surv.beta0.se[tmat.i])
pvec.samples[i,'surv.beta1'] <- rnorm(1, pvec$surv.beta1[tmat.i],
pvec$surv.beta1.se[tmat.i])
pvec.samples[i,'growth.beta0'] <- rnorm(1, pvec$growth.beta0[tmat.i],
pvec$growth.beta0.se[tmat.i])
pvec.samples[i,'growth.beta1'] <- rnorm(1, pvec$growth.beta1[tmat.i],
pvec$growth.beta1.se[tmat.i])
pvec.samples[i,'growth.sigma'] <- pvec$growth.sigma[tmat.i]
pvec.samples[i,'growth.var.exp'] <- pvec$growth.var.exp[tmat.i]
pvec.samples[i,'fl.beta0'] <- rnorm(1, pvec$fl.beta0[tmat.i], pvec$fl.beta0.se[tmat.i])
pvec.samples[i,'fl.beta1'] <-rnorm(1, pvec$fl.beta1[tmat.i],pvec$fl.beta1.se[tmat.i])
pvec.samples[i,'seed.beta0'] <- rnorm(1, pvec$seed.beta0[tmat.i],
pvec$seed.beta0.se[tmat.i])
pvec.samples[i,'seed.beta1'] <- rnorm(1, pvec$seed.beta1[tmat.i],
pvec$seed.beta1.se[tmat.i])
pvec.samples[i,'recruit.mean'] <- pvec$recruit.mean[tmat.i]
pvec.samples[i,'recruit.var'] <- pvec$recruit.var[tmat.i]
pvec.samples[i,'p.est'] <- pvec$p.est[tmat.i] / p.est.mean #this is not yet p.est, but the
factor to multiple # dd.p.est by!!!

}
for(i in 2:no.years){
year.step.temp <- year.step(
Nt0=Nts[,,i-1],
Seeds0=Seedss[,i-1],
disp.prob.mat=disp.prob.mat,
no.subpops=no.subpops,
pvec.samples=pvec.samples,
```

```
                                        max.size=max.size,
                                        bigM=bigM,
                                        prob.pos.cor=prob.pos.cor,
                                        no.tmats=no.tmats,
                                        prob.bad=prob.bad,
                                        good.bad=good.bad,
                                        spatial.sd=spatial.sd,
                                        spatial.coef=spatial.coef,
                                        disp.dist.matrix=disp.dist.matrix,
                                        )
                        Nts[,,i] <- year.step.temp$Nt1
                        Nts.sum[i] <- sum(Nts[,,i])
                        Seedss[,i] <- year.step.temp$Seeds1
                        points(i, Nts.sum[i])
                }
                return(Nts.sum)
}

#============================================================
# Dispersal functions(power, power.norm, seed.rain)
#============================================================
power <- function(x,a=1){
                        (1/x)^a
                }
# Inputs
# a = the exponent term in the inverse power function. This is set to one to give the curve
#of the function the shape we desire (most seeds falling near parent population, which
#makes biological sense (e.g., Reed's Paradox).
# min = half the length of the patch size
# x = vector of distances
# Output
# Vector of probabilities of dispersal at distances x.
power.norm <- function(a=1,x, min){
                        norm <- integrate(power,a=1,lower=min,upper=10000000)$value
                        out <- power(a=a,x=x)/norm
                        out
                }
# The seed.rain function requires the power and power.norm functions.
# Inputs:
# percent.disp = the percent of seeds dispersing from the subpopulation
# habitat.width = patch length
# distance = distance between two subpopulations (calculated from disp.dist.matrix)
# starting distance = edge of patch (half of the length of the habitat patch in the
#Pedicularis model)
```

```
# a =  the exponent term in the inverse power function. This is set to one to give the curve
#of the function the shape we desire (most seeds falling near parent population, which
#makes biological sense.
# Output
# A scalar giving the probability of dispersing seeds from a particular subpopulation
#reaching the particular habitat patch of interest.

seed.rain <- function(percent.disp,habitat.width, distance, starting.distance, a=1){
                if(percent.disp > 0){
  prob.disp <- (integrate(power.norm, min = starting.distance, a = a, lower = (distance -
                  (habitat.width/2)), upper = distance+(habitat.width/2)))
                        prob.disp <- percent.disp*prob.disp$value
                        if(unidirectional.dispersal==FALSE){
                                prob.disp <- prob.disp / 2
                        } else {
                                prob.disp <- prob.disp
                        }
                }else{
                        prob.disp <- 0
                }
                prob.disp
        }
#=============================================================
# step.dispersal - steps through a range of dispersal probabilities for the simulations
#=============================================================
# Inputs:
#  no.years = number of years to iterate the model
#  Nt0 = a vector representing the initial size distribution. The length of this vector should
#equal bigM.
#  Seeds0 = a vector containing the initial number of seeds produced by each site. The
#length of this vector should
#         equal the number of sites.
#  disp.prob.mat = a site x site dispersal probability matrix
#  pvec = a list of the estimates of the regressions for each vital rate
#  max.size = the maximum observed size of an individual in the population
#  bigM = the number of meshpoints in the iteration matrix (in the Pedicularis example
#bigM = 100)
#  no.subpops = the number of sites (or subpopulations)
#  prob.pos.cor = the probability of positive correlation (a value between 0 and 1)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each year and site for the three sites with more than one plant)
#  prob.bad = the probability of a catastrophe or 'bad' year (a value between 0 and 1)
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
```

```
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations
#  no.reps = number of replications
#  log = if 'TRUE' then the dispersal probabilities are on a log10 scale.
#  ext.threshold = value for the quasi-extinction theshold
#  habitat width = the size of the habitat patches. In this model patch size is constant.
#  starting distance = distance from center of patch where within patch dispersal falls off
#  upstream.fraction = the proportion of seeds that disperse upstream (a value between 0
#and 1)
# Output
# A list containing the probabilities of quasi-extinction for corresponding probabilities of
#dispersal.
step.dispersal <- function(
                    no.years,
                    Nt0,
                    Seeds0,
                    no.subpops,
                    pvec,
                    max.size,
                    bigM,
                    prob.pos.cor,
                    prob.bad,
                    good.bad,
                    spatial.sd,
                    spatial.coef,
                    no.tmats,
                    p.disp.stepsize,
                    p.disp.min,
                    p.disp.max,
                    patch.size,
                    no.reps,
                    disp.dist.matrix,
                    log=FALSE,
                    ext.threshold,
                    habitat.width,
                    starting.distance,
                    upstream.fraction=.1
                    ){

          if(!log){
                    p.disp.steps<-seq(from = p.disp.min, to = p.disp.max, by = p.disp.stepsize)
          }else{
         p.disp.steps<-10^seq(from = log10(p.disp.min), to = log10(p.disp.max), by =
                                        log10(p.disp.stepsize) )
                    #here step gives the factor for multiplication, not a fixed interval
```

```
	}

	num.steps <- length(p.disp.steps)
	p.ext.output <-
matrix(NA,nrow=num.steps,ncol=3,dimnames=list(NULL,c('mean','lower.95.ci','upper.9
5.ci')))
# Column 1 is the mean, columns 2 and 3 are the lower and upper 95% confidence
#intervals, respectively.
	for(i in 1:num.steps){
		p.disp.temp <- p.disp.steps[i]
					disp.matrix.temp <-
	 matrix(NA,nrow=dim(disp.dist.matrix)[1],ncol=dim(disp.dist.matrix)[2])

		for(j in 1:no.subpops){
			for(k in 1:no.subpops){
				if(j==k){
					disp.matrix.temp[j,k] <- 1
				}else{
					disp.matrix.temp[j,k] <- seed.rain(
							percent.disp = p.disp.temp,
							habitat.width = habitat.width,
							distance = disp.dist.matrix[j,k],
							starting.distance = starting.distance
							)
				}
			}
		}

					direction.matrix <-
	 matrix(NA,nrow=dim(disp.dist.matrix)[1],ncol=dim(disp.dist.matrix)[2])
		diag(direction.matrix)<- 1
	 direction.matrix[upper.tri(disp.matrix.temp,diag=FALSE)] <- upstream.fraction
	direction.matrix[lower.tri(disp.matrix.temp,diag=FALSE)] <- 1-upstream.fraction
		disp.matrix.temp <- disp.matrix.temp * direction.matrix
		prob.ext <- numeric(no.reps)
		for(m in 1:no.reps){
	print(paste('pos.cor=',prob.pos.cor,' p.disp=',p.disp.temp,' p.bad=',prob.bad))
			N.iter.temp <- step.many.years(
				no.years=no.years,
				Nt0=Nt0,
				pvec=pvec,
				Seeds0=Seeds0,
				no.tmats=no.tmats,
				prob.bad=prob.bad,
				good.bad=good.bad,
				spatial.sd=spatial.sd,
```

```
                                spatial.coef=spatial.coef,
                                disp.prob.mat=disp.matrix.temp,
                                no.subpops=no.subpops,
                                max.size=max.size,
                                bigM=bigM,
                                prob.pos.cor=prob.pos.cor,
                                disp.dist.matrix=disp.dist.matrix
                        )
                        N.min.temp <- min(N.iter.temp[2:no.years])
                        prob.ext[m] <- ifelse(N.min.temp<ext.threshold,1,0)
                }

        p.ext.output[i,1] <- mean(prob.ext)
        p.ext.output[i,2] <- quantile(prob.ext,probs=.0275)
        p.ext.output[i,3] <- quantile(prob.ext,probs=.975)
        }
        if(log){
    plot(p.ext.output[,1]~p.disp.steps,xlab='probability of dispersal',ylab='probability of
                                        extinction',log='x')
        }else{
    plot(p.ext.output[,1]~p.disp.steps,xlab='probability of dispersal',ylab='probability of
                                        extinction')
        }
        return(list(p.extinction=p.ext.output,p.dispersal=p.disp.steps))
}
#============================================================
# step.prob.bad - steps through a range of probabitlies of extreme events and
#       through a range of dispersal probabilities
#============================================================#
#Inputs:
#  no.years = number of years to iterate the model
#  Nt0 = a vector representing the initial size distribution. The length of this vector should
#equal bigM.
#  Seeds0 = a vector containing the initial number of seeds produced by each site. The
#length of this #vector should
#       equal the number of sites.
#  disp.prob.mat = a site x site dispersal probability matrix
#  pvec = a list of the estimates of the regressions for each vital rate
#  max.size = the maximum observed size of an individual in the population
#  bigM = the number of meshpoints in the iteration matrix (in the Pedicularis example
#bigM = 100)
#  no.subpops = the number of sites (or subpopulations)
#  prob.pos.cor = the probability of positive correlation (a value between 0 and 1)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each #year and site for the three sites with more than one plant)
#  prob.bad = the probability of a catastrophe or 'bad' year (a value between 0 and 1)
```

```
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations
#  no.reps = number of replications
#  log = if 'TRUE' then the dispersal probabilities are on a log10 scale.
#  ext.threshold = value for the quasi-extinction theshold
#  habitat width = the size of the habitat patches. In this model patch size is constant.
#  starting distance = distance from center of patch where within patch dispersal falls off
#  upstream.fraction = the proportion of seeds that disperse upstream (a value between 0
#and 1)
#  prob.bad.step.size = interval size of steps through the range of probabilies of extreme
#events
#  prob.bad.min = the minimum probabilitity of an extreme event
#  prob.bad.max = the maximum probability of an extreme event
#  path = name of file path to which outputs will be written as .csv files
# Output
# A matrix containing the probabilities of quasi-extinction for corresponding probabilities
#of extreme #events and probabilities of dispersal.
# This matrix is written as a .csv file to the directory specified by path.

step.prob.bad <- function(
                    no.years,
                    Nt0,
                    Seeds0,
                    no.subpops,
                    pvec,
                    max.size,
                    bigM,
                    prob.pos.cor,
                    no.tmats,
                    good.bad,
                    spatial.sd,
                    spatial.coef,
                    p.disp.stepsize,
                    p.disp.min,
                    p.disp.max,
                    patch.size,
                    no.reps,
                    disp.dist.matrix,
                    log=FALSE,
                    ext.threshold,
                    habitat.width,
```

```
                starting.distance,
                prob.bad.step.size,
                prob.bad.min,
                prob.bad.max,
                path){

                        if(!log){
        p.disp.steps<-seq(from = p.disp.min, to = p.disp.max, by = p.disp.stepsize)
                        }else{
      p.disp.steps<-10^seq(from = log10(p.disp.min), to = log10(p.disp.max), by =
                                log10(p.disp.stepsize) )
                                #here step gives the factor for multiplication, not a fixed
                                #interval
                        }
                        load(file=paste(path,'runcount',sep=''))
                        runcount <- runcount+1
                        save(runcount,file=paste(path,'runcount',sep=''))
prob.bad.steps<-seq(from = prob.bad.min, to = prob.bad.max, by = prob.bad.step.size)
                        num.bad.steps <- length(prob.bad.steps)
    prob.bad.output <- matrix(NA, nrow= num.bad.steps, ncol=length(p.disp.steps),

        dimnames=list(prob.bad.steps,p.disp.steps)
                                                )
                        for(i in 1:num.bad.steps){
                                dispersal.out.temp <- step.dispersal(
                                                no.years=no.years,
                                                Nt0=Nt0,
                                                Seeds0=Seeds0,
                                                no.subpops=no.subpops,
                                                pvec=pvec,
                                                max.size=max.size,
                                                bigM=bigM,
                                                prob.pos.cor=prob.pos.cor,
                                                no.tmats=no.tmats,
                                                prob.bad=prob.bad.steps[i],
                                                good.bad=good.bad,
                                                spatial.sd=spatial.sd,
                                                spatial.coef=spatial.coef,
                                                p.disp.stepsize=p.disp.stepsize,
                                                p.disp.min=p.disp.min,
                                                p.disp.max=p.disp.max,
                                                patch.size=patch.size,
                                                no.reps=no.reps,
                                                disp.dist.matrix=disp.dist.matrix,
                                                log=TRUE,
                                                ext.threshold=ext.threshold,
```

```
                                                habitat.width=habitat.width,
                                                starting.distance=starting.distance)
                        prob.bad.output[i,] <- dispersal.out.temp$p.extinction[,1]
write.csv(prob.bad.output,paste(path,"prob_bad_test_cor",prob.pos.cor,"run",runcount,".c
                                        sv",sep=''),row.names=TRUE)
                                         }
                    return(prob.bad.output=prob.bad.output)
}
#============================================================
# step.prob.cor - steps through a range of dispersal probabilities, probabilities
#         of extreme events, and probabilities of positive correlations in vital rates between
#         patches
#============================================================
# Inputs:
#  no.years = number of years to iterate the model
#  Nt0 = a vector representing the initial size distribution. The length of this vector should
#equal bigM.
#  Seeds0 = a vector containing the initial number of seeds produced by each site. The
#length of this #vector should equal the number of sites.
#  disp.prob.mat = a site x site dispersal probability matrix
#  pvec = a list of the estimates of the regressions for each vital rate
#  max.size = the maximum observed size of an individual in the population
#  bigM = the number of meshpoints in the iteration matrix (in the Pedicularis example
#bigM = 100)
#  no.subpops = the number of sites (or subpopulations)
#  no.tmats = the number of transition matrices (in the Pedicularis example there are six,
#one for each #year and site for the three sites with more than one plant)
#  prob.bad = the probability of a catastrophe or 'bad' year (a value between 0 and 1)
#  good.bad = a vector that specifies, which transition matrices are considered 'good' or
#'bad'
#  spatial.sd = the standard deviation of a gaussian function describing the spatial
#autocorrelation kernel
#  spatial.coef = the coefficient that sets the strength of spatial autocorrelation, between 0
#and 1
#  disp.dist.matrix = a matrix giving all pairwise distances between subpopulations
#  no.reps = number of replications
#  log = if 'TRUE' then the dispersal probabilities are on a log10 scale.
#  ext.threshold = value for the quasi-extinction theshold
#  habitat width = the size of the habitat patches. In this model patch size is constant.
#  starting distance = distance from center of patch where within patch dispersal falls off
#  upstream.fraction = the proportion of seeds that disperse upstream (a value between 0
#and 1)
#  prob.bad.step.size = interval size of steps through the range of probabilies of extreme
#events
#  prob.bad.min = the minimum probabilitity of an extreme event
#  prob.bad.max = the maximum probability of an extreme event
```

```
#  path = name of file path to which outputs will be written as .csv files
#  name = name to be given to output
#  prob.pos.cor.stepsize = interval size of steps through the range of probabilies of
#positive correlations #in vital rates
#  prob.pos.cor.min = the minimum probabilitity of positive correlation
#  prob.pos.cor.max = the maximum probability of an positive correlation
# Output
# An array containing the probabilities of quasi-extinction for corresponding probabilities
#of extreme #events, probabilities of dispersal
# and probabilities of correlations in vital rates between patches.
# This matrices in this array are written as .csv files to the directory specified by path.

step.prob.cor <- function(
                    no.years,
                    Nt0,
                    Seeds0,
                    no.subpops,
                    pvec,
                    max.size,
                    bigM,
                    prob.pos.cor.stepsize,
                    prob.pos.cor.min,
                    prob.pos.cor.max,
                    no.tmats,
                    prob.bad,
                    good.bad,
                    spatial.sd,
                    spatial.coef,
                    p.disp.stepsize,
                    p.disp.min,
                    p.disp.max,
                    patch.size,
                    no.reps,
                    disp.dist.matrix,
                    log.disp=FALSE,
                    ext.threshold,
                    habitat.width,
                    starting.distance,
                    prob.bad.step.size,
                    prob.bad.min,
                    prob.bad.max,
                    path,
                    name=''){
                            if(!log){
          p.disp.steps<-seq(from = p.disp.min, to = p.disp.max, by = p.disp.stepsize)
                            }else{
```

```
p.disp.steps<-10^seq(from = log10(p.disp.min), to = log10(p.disp.max), by =
                     log10(p.disp.stepsize) )
                #here step gives the factor for multiplication, not a fixed
                #interval
        }
        load(file=paste(path,'runcount',sep=''))
        runcount <- runcount+1
        save(runcount,file=paste(path,'runcount',sep=''))

prob.bad.steps<-seq(from = prob.bad.min, to = prob.bad.max, by = prob.bad.step.size)
        num.bad.steps <- length(prob.bad.steps)
prob.pos.cor.steps <- seq(from = prob.pos.cor.min, to = prob.pos.cor.max, by =
                          prob.pos.cor.stepsize)
        num.cor.steps <- length(prob.pos.cor.steps)
prob.cor.output <- array(NA, dim=c(num.bad.steps, length(p.disp.steps), num.cor.steps),

    dimnames=list(prob.bad.steps,p.disp.steps,prob.pos.cor.steps))
        for(i in 1:num.cor.steps){
                cor.output.temp <- step.prob.bad(
                        no.years=no.years,
                        Nt0=Nt0,
                        Seeds0=Seeds0,
                        no.subpops=no.subpops,
                        pvec=pvec,
                        max.size=max.size,
                        bigM=bigM,
                        prob.pos.cor=prob.pos.cor.steps[i],
                        no.tmats=no.tmats,
                        good.bad=good.bad,
                        spatial.sd=spatial.sd,
                        spatial.coef=spatial.coef,
                        p.disp.stepsize=p.disp.stepsize,
                        p.disp.min=p.disp.min,
                        p.disp.max=p.disp.max,
                        patch.size=patch.size,
                        no.reps=no.reps,
                        disp.dist.matrix=disp.dist.matrix,
                        log,
                        ext.threshold=ext.threshold,
                        habitat.width=habitat.width,
                        starting.distance=starting.distance,
                        prob.bad.step.size=prob.bad.step.size,
                        prob.bad.max = prob.bad.max,
                        prob.bad.min = prob.bad.min,
                        path=path)
                prob.cor.output[,,i] <- cor.output.temp
```

```
        save(prob.cor.output,file=paste(path,"cor_test_run",name,sep=''))
                                }
                                for(disp.num in 1:length(p.disp.steps)){
write.csv(prob.cor.output[,disp.num,],file=paste(path,'cor_test_Disp',disp.num,'_run',runc
                                ount,name,'.csv',sep=''),row.names=FALSE)
                                }
                        return(p.bad_by_p.disp_by_pos.cor=prob.cor.output)
}

# End.
```

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