Biological Conservation 155 (2012) 202–211

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Effects of a non-native biocontrol weevil, *Larinus planus*, and other emerging threats on populations of the federally threatened Pitcher's thistle, *Cirsium pitcheri*

Kayri Havens [a,*], Claudia L. Jolls [a,b,c], Julie E. Marik [b], Pati Vitt [a], A. Kathryn McEachern [d], Darcy Kind [e]

[a] Division of Plant Science and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA
[b] Department of Biology, East Carolina University, Greenville, NC 27858-4353, USA
[c] University of Michigan Biological Station, 9133 Biological Road, Pellston, MI 49769, USA
[d] U.S. Geological Survey – Western Ecological Research Center, Channel Islands Field Station, 1901 Spinnaker Drive, Ventura, CA 93001-4354, USA
[e] Wisconsin Department of Natural Resources, Bureau of Endangered Resources, 101 S. Webster St., Madison, WI 53704, USA

ARTICLE INFO

Article history:
Received 30 January 2012
Received in revised form 6 June 2012
Accepted 9 June 2012
Available online 27 July 2012

Keywords:
Biocontrol impacts
Weevil
Demography
Larinus planus
Cirsium pitcheri
Seed predation

ABSTRACT

Larinus planus Frabicius (Curculionidae), is a seed-eating weevil that was inadvertently introduced into the US and was subsequently distributed in the US and Canada for the control of noxious thistle species of rangelands. It has been detected recently in the federally threatened Pitcher's thistle (*Cirsium pitcheri*). We assayed weevil damage in a natural population of Pitcher's thistle at Whitefish Dunes State Park, Door County, WI and quantified the impact on fecundity. We then estimated the impact of this introduced weevil and other emerging threats on two natural, uninvaded populations of Pitcher's thistle for which we have long-term demographic data for 16 yr (Wilderness State Park, Emmet County, MI) and 23 yr (Miller High Dunes, Indiana Dunes National Lakeshore, Porter County, IN). We used transition matrices to determine growth rates and project the potential effects of weevil damage, inbreeding, goldfinch predation, and vegetative succession on Pitcher's thistle population viability. Based on our models, weevil seed predation reduced population growth rate by 10–12%, but this reduction was enough to reduce time to extinction from 24 yr to 13 yr and 8 yr to 5 yr in the MI and IN population, respectively. This impact is particularly severe, given most populations of Pitcher's thistle throughout its range hover near or below replacement. This is the first report of unanticipated ecological impacts from a biocontrol agent on natural populations of *Cirsium pitcheri*.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

1.1. Pitcher's thistle system and threats

Cirsium pitcheri Torr. and Gray, Pitcher's thistle (Asteraceae) is a monocarpic perennial of the shorelines of the upper Great Lakes along Lakes Huron, Michigan, and Superior in the US and Canada (Fig. 1). This species was federally listed as threatened in 1988 (USFWS, 1988). *C. pitcheri* requires open, early successional, disturbance-prone habitats and typically is found on dunes and sandy, cobble shores with 30% vegetative cover or less (Hamzé, 1998; McEachern, 1992). Pitcher's thistle is relatively short-lived; it typically grows 4–8 yr, flowers once, then dies. Flowering stems bolt to a height of approximately 1 m in May then flower from late June to early September, producing 1–35 pink to creamy-white capitula, or flower heads, per plant, which produce an average of 85 protandrous disk florets per head. Capitulum production varies among sites and years (Hamzé and Jolls, 2000) and is related to plant size (D'Ulisse and Maun, 1996; Jolls and Lin, Unpublished results). *C. pitcheri* is insect-pollinated with a mixed-mating system; seed set appears tied to pollinator activity, whether selfing or outcrossing (Loveless, 1984; McEachern, 1992). This thistle species lacks vegetative modes of reproduction; therefore, seed production and successful seedling recruitment (ecesis) are critical. Population growth can be retarded by deleterious effects on seed production, germination, seedling and/or adult survival from factors such as shading or litter accumulation from natural succession or invasive plants as well as herbivory on both seeds and plants (Marik, 2007; Jolls et al., in preparation).

In the US, natural stands of Pitcher's thistle occur in Michigan, Wisconsin, and Indiana; reintroductions have occurred in Illinois, Indiana, and Wisconsin. The majority of Pitcher's thistle populations occur in Michigan along the north and northeast shores of Lake Michigan (173 elemental occurrences, USFWS, 2002). Threats to *C. pitcheri* include habitat destruction, human disturbance from shoreline recreation, as well as direct and indirect effects from non-native plant species, including baby's breath (*Gypsophila*

* Corresponding author. Tel.: +1 847 835 8378, fax: +1 847 835 5484.
E-mail addresses: khavens@chicagobotanic.org (K. Havens), jollsc@ecu.edu (C.L. Jolls), marikj@ecu.edu (J.E. Marik), pvitt@chicagobotanic.org (P. Vitt), kathryn_mceachern@usgs.gov (A.K. McEachern), Darcy.kind@wisconsin.gov (D. Kind).

0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2012.06.010

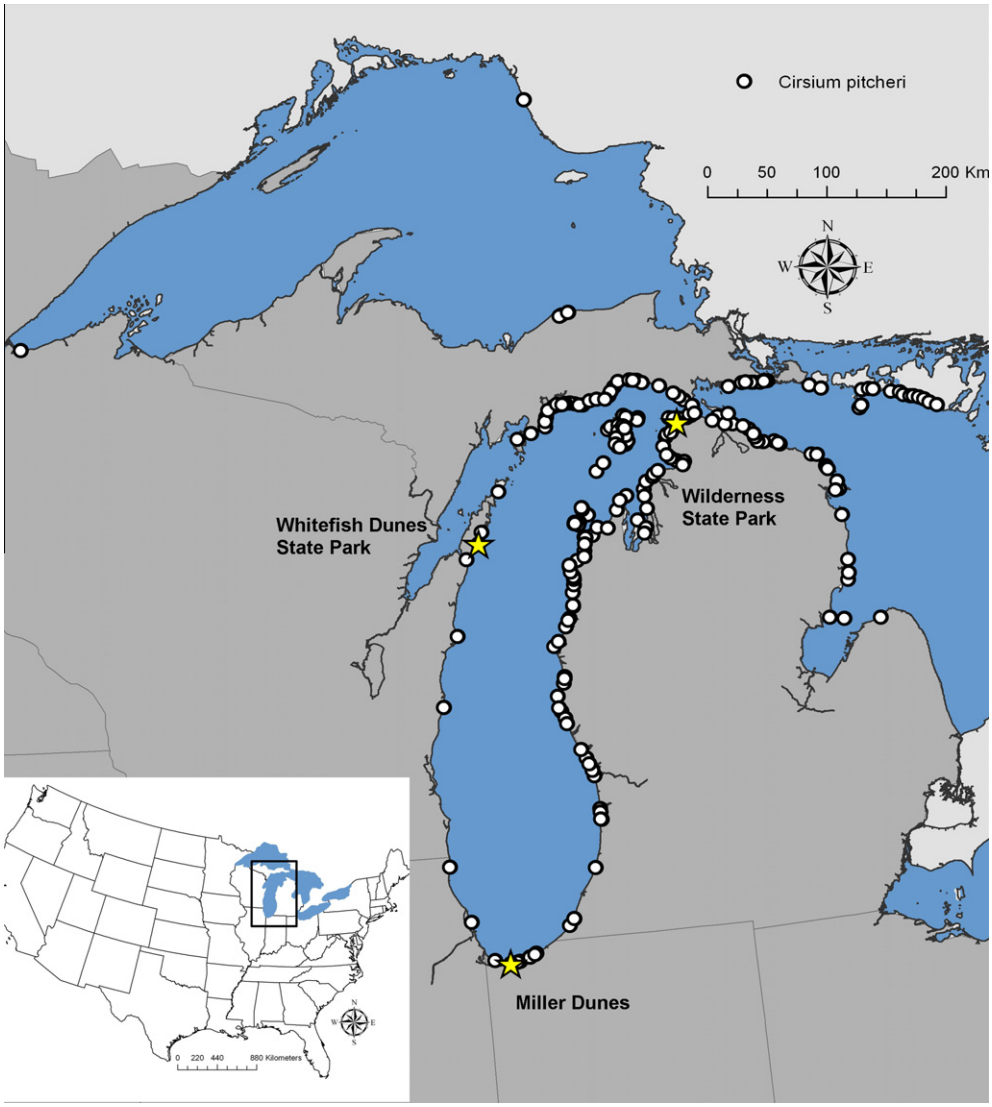

Fig. 1. Map of *Cirsium pitcheri* occurrences (dots) and locations of populations used in this study (stars).

paniculata L.; Hamzé and Jolls, 2000; Jolls et al., in preparation), spotted knapweed (*Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek; Baskett et al., 2011), Lombardy poplar (*Populus nigra* L.; USFWS, 2010) and Austrian pine (*Pinus nigra* ssp. *austriaca* (Hoss) Bid.; Leege and Murphy, 2001). Native mammals and birds also pose threats, including herbivory and trampling from white-tailed deer (*Odocoileus virginianus*; Pellerin et al., 2006), 13-lined ground squirrel (*Spermophilus tridecemlineatus*; Loveless, 1984), Eastern cottontail rabbit (*Sylvilagus floridanus*; McEachern, 1992), and American goldfinch (*Carduelis tristis*; Loveless, 1984; McEachern, Unpublished results). Insects can damage plants, including apical meristem damage from spittlebugs (Cercopidae; Bevill et al., 1999) and the artichoke plume moth (*Platyptilia carduidactyla*; Bevill et al., 1999). Lastly, climate change is predicted to significantly restrict the range of *C. pitcheri* over the next several decades (Vitt et al., 2010).

1.2. Biocontrol weevil history

Two species of seed weevils introduced or distributed for biocontrol of Canada and musk thistles (*Cirsium arvense* and *Carduus nutans*, respectively) have now been found to impact *C. pitcheri*. *Rhinocyllus conicus* Frölich was introduced from Europe in 1969 to control *Carduus* spp., especially *C. nutans* L. This weevil will feed on 22 native thistles and its potential to impact on the federally threatened Pitcher's thistle was reported as early as 1997 (Louda et al., 1997). *R. conicus* has been documented to have the potential to drive the closely related endemic sand hills thistle, *Cirsium canescens* to extinction (Louda et al., 2003; Rose et al., 2005). This weevil was discovered in a common garden at Chicago Botanic Garden in 2007, feeding on seed heads of *C. pitcheri*. The weevil was found in approximately 40% of the heads, reducing seed set by 95% in those heads in the first year of infestation. *R. conicus* has been observed on *Carduus nutans* at both the south and north units of Illinois Beach State Park, but has not yet been detected in the *Cirsium pitcheri* reintroduction there. *R. conicus* has not been found in any natural populations of *C. pitcheri* to date.

Larinus planus Frabicius (tribe Lixini, subfamily Lixinae, Curculionidae, syn. *Hadroplantus planus*) is a seed eating weevil from Eurasia that is thought to have entered the US accidentally in the 1960s, first reported in Maryland in 1971 (White, 1972; Wheeler and Whitehead, 1985; Cripps et al., 2011). It is thus adventive to the US. Louda and O'Brien (2002) and Dodge (2005) provide details of the taxonomy, ecology, spread, and impact of *L. planus* on western thistles and it has been found in at least three species of native thistles in western states (Louda et al., 2003). Although *L. planus*

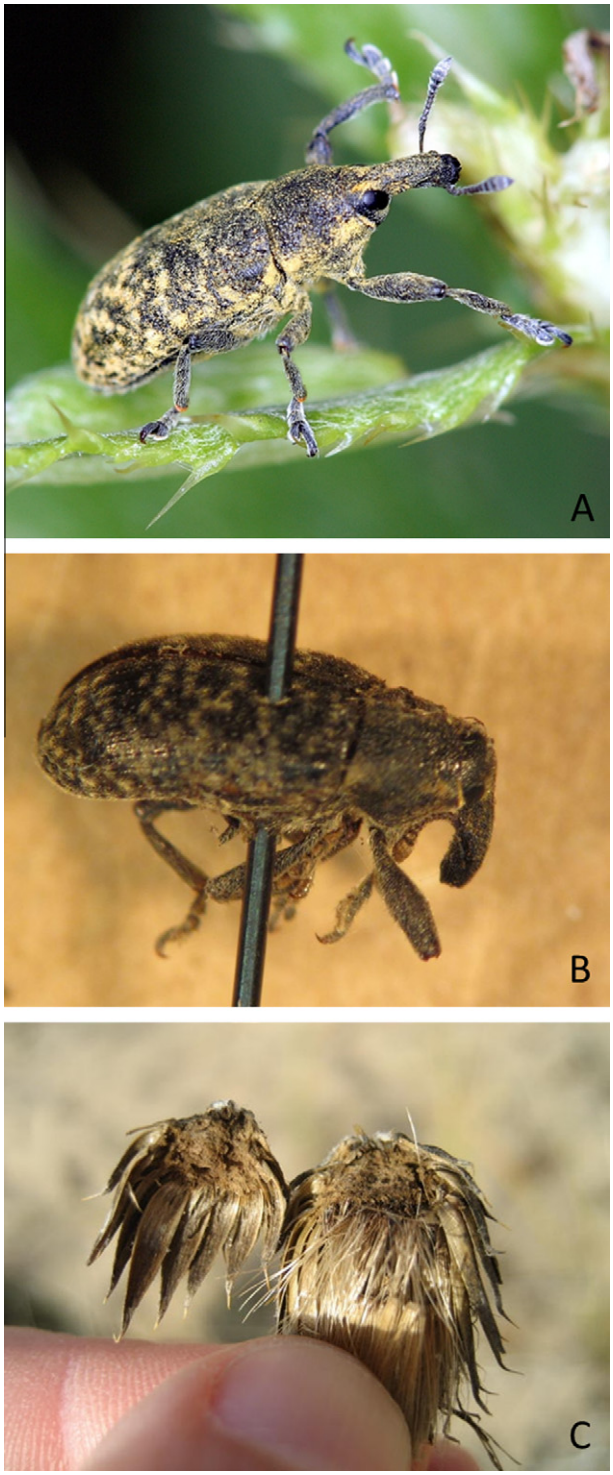

Fig. 2. A. Adventive biological control Canada thistle bud weevil (*Larinus planus*, Curculionidae). Photograph by David Cappaert, Michigan State University, Lansing, MI. B. *Larinus planus* collected on *Cirisum pitcheri* at Whitefish Dunes State Park, WI and vouchered at Chicago Botanic Garden. Photograph by Jim Steffen, Chicago Botanic Garden. C. *Cirsium pitcheri* flower head damaged by *Larinus planus*. Photograph by Darcy Kind, Wisconsin Department of Natural Resources.

was not deliberately introduced to the US, it has been actively redistributed for biocontrol use against Canada thistle (*Cirsium arvense*) in several states. Because the weevil was adventive, no permits were required for its redistribution and it is not possible to know how extensive the human-mediated movement has been. We first found *L. planus* in the Whitefish Dunes State Park (WDSP, Door Co., WI) population of *Cirsium. pitcheri* in 2010 while collecting seed for banking for long term conservation (Havens, Personal observation; Fig. 2). In 2010, the weevil was found in about one-third of the seed heads examined; viable seeds were not found in those heads. In 2011, we conducted a more extensive survey of the Whitefish Dunes population and the weevil was found in over half the seed heads and almost no viable seed was found in those heads. Subsequently, the Wisconsin Department of Natural Resources surveyed populations of Pitcher's thistle on public and private lands throughout the Door Peninsula and *Larinus. planus* was found in every known thistle population in the County, including those on Washington Island (Kind, Personal observation). This is the first report of a biocontrol weevil in natural populations of *C. pitcheri* anywhere throughout its range. The infestation is likely quite recent because no weevils were detected during a 2007 seed collection made at Whitefish Dunes State Park (Havens, Personal observation).

1.3. Goals of this study

This work is part of a larger project that includes five natural and four restored populations throughout the range of *C. pitcheri* (Fant et al., in preparation; Jolls et al., in preparation). We ask what ecological and genetic factors might be responsible for changes in population growth rates of this species and how these factors might impact population viability. The objectives of the work we report here are (1) to determine the extent of the *L. planus* infestation in a natural population of Pitcher's thistle in Door County, WI and (2) to ask what might be the effect of weevil seed predation and other threats on thistle population growth and viability?

2. Materials and methods

2.1. Survey of weevil impacts in Door County, WI

After discovering *L. planus* in *C. pitcheri* at Whitefish Dunes State Park in 2010, we conducted a survey to determine the extent of weevil impact. On September 29, 2011, after all seeds had matured, we laid out five non-overlapping 30 m transects through the *C. pitcheri* population. Transect locations were selected haphazardly on dunes where *C. pitcheri* was present. We randomly selected a start point on each transect between 1 and 10 m and then examined every plant within a 5 m band to either side of the transect. For each flowering plant, we counted the number of flower heads, measured the diameter of each head, noted its position (main branch terminal flower head, lateral branch terminal flower head or lateral flower head) then dissected it to look for weevil damage and to count the number of filled, intact seeds, if any, present. If seeds were present, they were dropped in place, mimicking natural dispersal. In non-weevil infested flower heads, most seeds had already dispersed. In weevil infested flower heads, the heads never opened fully to allow seed dispersal; seed remnants and weevil frass were found in a clump within the head, enclosed by the involucral bracts (phyllaries) (Fig. 2).

2.2. Demographic data set for Wilderness State Park, MI and Indiana Dunes National Lakeshore, IN

We have monitored natural populations of Pitcher's thistle at Sturgeon Bay Dunes, Wilderness State Park (WSP), Emmet County, MI between 1995 and 2011 (with the exception of 2001–2004) and at a site at Indiana Dunes National Lakeshore (INDL), a mid-successional open blowout slope in the Miller High Dunes complex (MIHI) between 1988 and 2011 (with the exception of 1995 and 1996). Demographic data in MI were collected by Jolls and

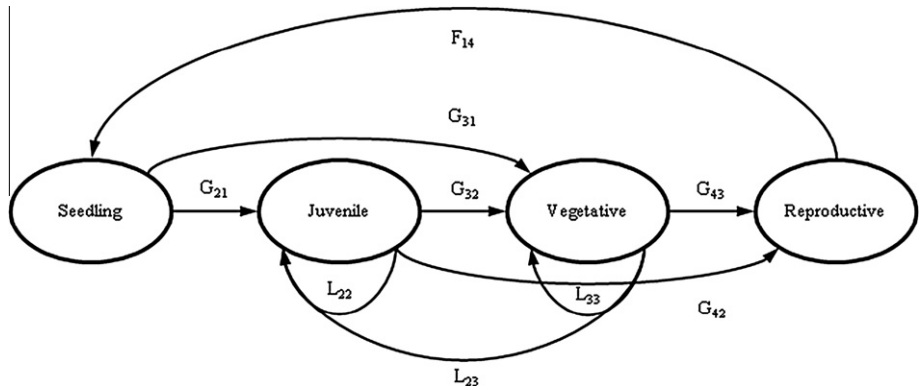

Fig. 3. Stage-based life cycle graph for *Cirsium pitcheri*. The arrows represent a possible transition between years. Matrix elements (F_{ij}, G_{ij}, L_{ij}, F_{14}) associated with the arrows correspond to the transition probabilities in stage-based projection matrices and are presented for growth (G_{ij}), stasis (L_{ij}), and sexual reproduction (F_{14}).

colleagues; McEachern and colleagues collected the IN data. *C. pitcheri* plants were tagged and measured at peak flowering, in a $40 \times 50\ m^2$ plot at WSP in middle July and in 0.10 hectare plots 1988–2011 at MIHI in late June. Individual plants were assigned to one of four stage-classes, based on leaf morphology: (1) seedling (both cotyledons are present), (2) juvenile (at least one true leaf has formed), (3) vegetative (leaves are all pinnatifid), and (4) reproductive (flowers are present). Stage-based approaches to population demography and projection have been used previously for natural and restored populations of *C. pitcheri* (McEachern, 1992; McEachern et al., 1994; Bell et al., 2003; Jolls et al., in preparation).

We used empirical transition matrices as a basis for simulation modeling studies intended to address how factors such as (1) seed predation from *Larinus* or native vertebrates such as the American Goldfinch (*Carduelis tristis*), (2) inbreeding and/or (3) increased shading and litter accumulation from natural succession or invasive species might affect population growth. We chose WSP because it is a particularly good surrogate to model the effects of the weevil at Whitefish Dunes State Park (WDSP) in WI. Both areas are extensive systems of continuous freshwater dunes supporting large populations of Pitcher's thistle. Both populations have nearly identical levels of genetic variability and inbreeding (Fant et al., in preparation). We also chose to model effects of the weevil at MIHI in INDL, a much smaller population of Pitcher's thistle at the southern limit of its range to contrast effects of the threats in populations of different sizes and settings.

Stage- (vs. size-) class models have been used extensively to study population dynamics of Pitcher's thistle (Bowles and McBride, 1996; Stanforth et al., 1997; Bell et al., 2003). We constructed stage-based Lefkovitch matrices using a life-cycle graph (Fig. 3) from 1995 to 2011 at WSP and 1988–2011 at MIHI (excluding years we did not sample). Population viability analysis was used to project the effects of *Larinus* and other factors as reductions in fecundity on *C. pitcheri* population growth and extinction risk. The population growth rate (λ) is the dominant eigenvalue produced by the transition matrix (Caswell, 2001); $\lambda > 1$ indicates a growing population and $\lambda < 1$, a population in decline. We used matrices from 16 WSP and 23 INDL transitions in the **popbio** package of Stubben and Milligan (2007), the R translation of the MATLAB code found in Caswell (2001) and Morris and Doak (2002).

2.3. Theory/calculation: modeling of fecundity reduction

We asked how different threats from seed predators, inbreeding, and increased vegetative cover from natural succession or invasive plants might impact population growth and viability. Previous elasticity analyses have showed that λ for *C. pitcheri* populations is sensitive to changes in fecundity element, seedling recruitment, as well as juvenile survivorship (Bell et al., 2003; Jolls et al., in preparation). We modeled the impact of a reduction in fecundity at four levels, corresponding to the four types of impact (weevil, goldfinch, inbreeding, shading and litter accumulation). Population viability and the stochastic rate of increase (λ_S) were determined using stage-based matrices. While average λ for all year-pairs cannot be calculated, the stochastic growth rate is an alternative (Morris and Doak, 2002; Tuljapurkar, 1982). The stochastic growth rate uses all measures of λ to approximate a long-term growth rate (λ_S) in a stochastic environment.

A viable population can be defined as having a probability of extinction (P_e) of <5% over the next 100 yr (Menges, 1990) or what we identify as the "5% Extinction Threshold" in the following graphs. We calculated the probability of extinction (P_e) for stage-based models assuming a population (1) in which density would not affect survivorship (density-independence), (2) occupying a stochastic environment, and (3) with a projection length of 500, 100, or 10 yr into the future (Caswell, 2001; Morris and Doak, 2002). For WSP, the 2011 population was used as the starting population vector and consisted of 453 seedlings (both cotyledons present), 59 juveniles (evidence of cotyledons even as scars and at least one true pinnatifid leaf formed), 355 vegetatives (all leaves pinnatifid), and 58 reproductives (flowering heads are present) ($N = 925$). For MIHI, the 2011 population was used as the starting population vector and consisted of 28 seedlings, 67 juveniles, 57 vegetatives, and 8 reproductives ($N = 160$ plants). P_e was calculated by randomly drawing from matrices with reduced seedling recruitment rates (F_{14} matrix element of Fig. 3) under simulated threats. Quasi-extinction rate was set at 30 individuals.

Matrices were selected at random with replacement and each matrix having an equal probability of being selected. We then conducted 10 runs of 5000 simulations each. We designated a quasi-extinction threshold of 30 individuals to alleviate effects of demographic stochasticity due to small population size (Morris and Doak, 2002). All populations containing fewer than 30 individuals were considered functionally extinct.

We further modeled changes in the fecundity element of matrices to project the finite rate of population increase for these natural populations under four scenarios of lowered recruitment from damage to seed or reduced germination and seedling establishment success. To simulate scenarios of different threats, we reduced the number of seedlings produced from each flowering adult the previous year. These reductions were based on field observations of decreased seed production and/or seedling success from our more than two decades of work on *C. pitcheri*.

These scenarios included reductions in the proportion of seedlings produced per flowering adult of the previous year as a result of (1) weevil invasion and seed depredation, (2) seed depredation

by finches, (3) inbreeding, and (4) succession that can reduce seedling establishment success through increases in shading and litter by native or invasive plant species. The first scenario reduced the proportion of seedlings produced per flowering adult of the previous year by 50% from weevil herbivory. Herbivory by the American goldfinch was estimated to reduce ecesis by 90% (McEachern, Unpublished results). We used a 75% reduction in the fecundity element in our matrices to estimate the effect of inbreeding on estimates of the population growth rate based on an earlier inbreeding depression study (Fant, Unpublished results). For the last scenario, the effects of increased shading and litter, from natural succession or non-native vegetation, were simulated by reducing the fecundity element by 34% (Marik, 2007; Jolls et al., in preparation).

These impacts were modeled singly and in all possible combinations as the products of independent probabilities to predict the stochastic population increase, λ_S and 95% confidence intervals, and P_e. We calculated these population parameters from simulation with the **popbio** package and **stoch.growth.rate** function (Caswell, 2001; Morris and Doak, 2002; Stubben and Milligan, 2007).

3. Results

3.1. Sampling for weevil occurrence in Door County, WI

A total of 501 capitula on 57 reproductive plants were examined. Only seven plants completely escaped weevil damage; fifty plants had at least one capitulum infested. In 226 of the capitula, seed was dispersed and no weevil damage observed (226/501 = 45%). Thirteen heads had no dispersed seed but also had no weevil damage. In 218 heads, weevils destroyed all of the seeds. In ten heads, weevil damage was present and one to three seeds appeared undamaged, but had not dispersed because weevil damage appeared to have prevented the head from fully opening. Thirty-four heads were very small, immature, and had not opened. At the time of our survey, 48% of the heads that matured (opened flowers) dispersed seed. It is possible that a few additional heads would have dispersed seed after our sampling date, so we estimated that the weevil reduced fecundity by 50% in 2011 and used that figure for our modeling. The weevil infestation at WDSP is relatively recent. Surveys for the weevil during a seed collection trip in 2007 did not find any weevil damage (Havens, Personal observation).

In both 2010 and 2011, several of the weevil infested flower heads had larva or adult weevils present. Four adult weevils were collected and subsequently identified by the Chicago Botanic Garden's ecologist, Jim Steffen, as *L. planus*. The insects were preserved and are maintained in the Garden's insect collection as voucher specimens (Fig. 2).

3.2. What is the effect of the weevil and other threats on population viability and time to extinction?

Population growth rates of these two monitored *C. pitcheri* populations are highly variable among years and sites, however, generally lambdas are below replacement ($\lambda < 1.0$) (Table 1). We calculated the stochastic growth rate to approximate long term population growth (Tuljapurkar, 1982; Morris and Doak, 2002). *C. pitcheri* populations at WSP and MIHI have years of population growth (Table 2), but overall, both sites are below replacement.

The addition of threats that reduce fecundity further reduces population growth, and the pattern is similar for both the larger, northern MI population and the smaller, southern IN population (Table 2). Weevil predation reduced population growth (λ) compared to natural field conditions, reducing the stochastic rate of population growth by 11.5% on average. Threats that had greater reductions in seed and seedling success (finch seed predation and inbreeding) reduced population growth rate more. Shading and litter accumulation from the course of natural succession or from invasive plants had the least impact on λ. As expected, seed depredation from weevils when combined with any other threat reduced population growth still further. Compared to the current

Table 1
Intrinsic rate of population growth (λ) for *Cirsium pitcheri* at two natural populations around Lake Michigan. NA = no data available.

Year-pair of monitoring	Wilderness State Park, MI (WSP) MI	Miller Dunes, IN
1988–1989	NA	0.780
1989–1990	NA	1.076
1990–1991	NA	0.998
1991–1992	NA	1.057
1992–1993	NA	0.642
1993–1994	NA	0.582
1994–1995	NA	NA
1995–1996	0.920	NA
1996–1997	0.671	NA
1997–1998	0.884	0.980
1998–1999	0.971	0.861
1999–2000	0.788	0.739
2000–2001	1.109	0.564
2001–2002	NA	0.939
2002–2003	NA	0.968
2003–2004	NA	0.492
2004–2005	NA	0.808
2005–2006	0.847	0.922
2006–2007	0.811	1.464
2007–2008	1.147	1.056
2008–2009	0.786	0.819
2009–2010	0.855	1.403
2010–2011	1.246	1.247
λ_S	0.926	0.976
(95% CI)	(0.924, 0.929)	(0.972, 0.980)

Table 2
The influence of seed predation by the biocontrol thistle head weevil, *Larinus planus*, singly and in combination with other emergent threats, on the finite rate of population increase (λ_S and 95% confidence intervals) natural populations of *Cirsium pitcheri* along northern Lake Michigan and at the southern limits of its range.

	Stochastic growth rate (λ_S) (95% CI)	
Scenario	Wilderness State Park, MI	Miller Beach, IN
Natural field conditions	0.9266 (0.9241, 0.9291)	0.9758 (0.9718, 0.9797)
Weevil predation	0.8255 (0.8240, 0.8272)	0.8561 (0.8534, 0.8588)
Finch predation	0.6917 (0.6910, 0.6924)	0.6773 (0.6761, 0.6786)
Inbreeding	0.7540 (0.7529, 0.7550)	0.7658 (0.7639, 0.7676)
Succession	0.8626 (0.8606, 0.8645)	0.9010 (0.8978, 0.9041)
Weevil, finch	0.6632 (0.6630, 0.6640)	0.6319 (0.6308, 0.6330)
Weevil, inbreeding	0.7038 (0.7030, 0.7045)	0.6960 (0.6947, 0.6974)
Weevil, succession	0.7792 (0.7780, 0.7805)	0.6484 (0.6472, 0.6495)
Weevil, finch, inbreeding	0.6377 (0.6372, 0.6383)	0.5821 (0.5810, 0.5832)
Weevil, finch, succession	0.6523 (0.6517, 0.6528)	0.6122 (0.6111, 0.6133)
Weevil, inbreeding, succession	0.6827 (0.6821. 0.6833)	0.6623 (0.6611, 0.6636)
Weevil, finch, inbreeding, succession	0.6339 (0.6333, 0.6344)	0.5741 (0.5730, 0.5753)

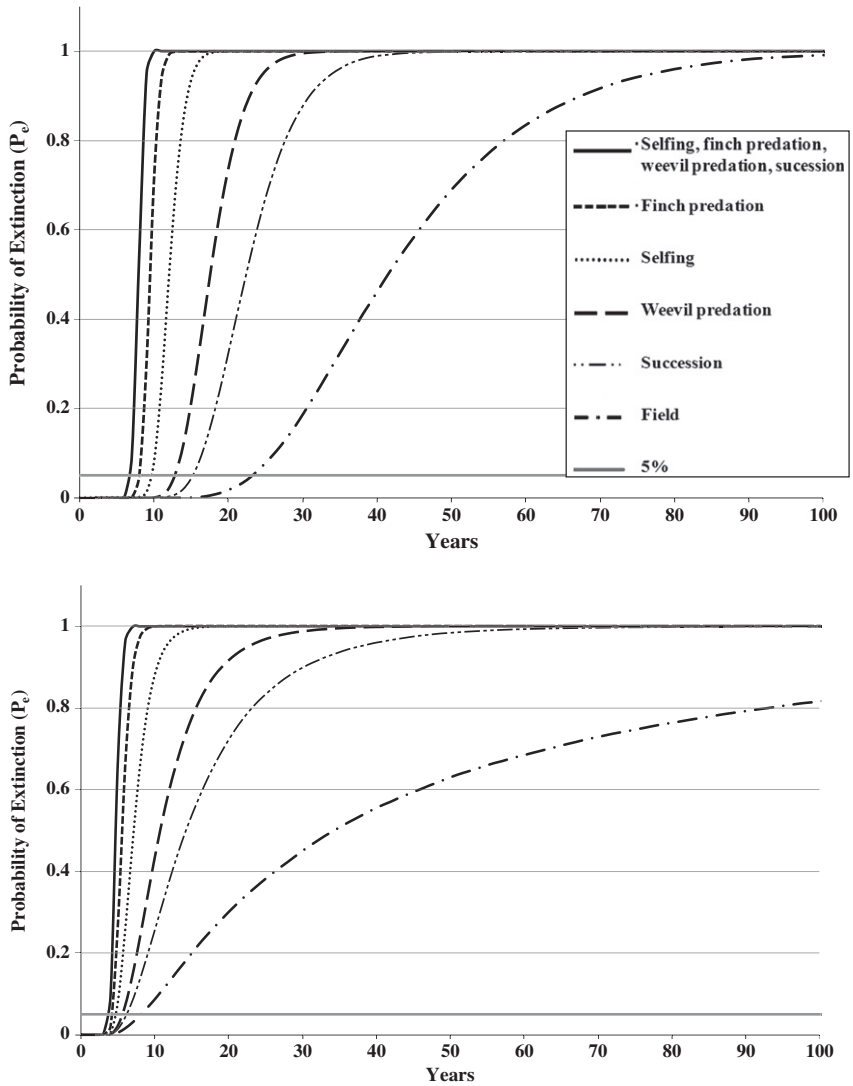

Fig. 4. Probability of extinction (P_e) for two natural populations of *Cirsium pitcheri* at Wilderness State Park, northern Michigan (top panel) and Miller High Dune, Indiana Dunes National Lakeshore (bottom panel) exposed to seed predation by weevil and four other threats, singly and in combination. Projections were carried out for 100 yr.

field conditions, all four threats, singly or in concert, dramatically reduce population growth rate.

No simulated population was viable, in the strict sense of a probability of extinction of less than 5% in 100 yr (Fig. 4). The probability of extinction in uninfested populations of *C. pitcheri* at WSP began to exceed the 5% viability threshold at 24 yr and 50% at 42 yr (Fig. 4). The WSP population is projected to have a 100% probability of extinction in 175 yr under observed field conditions. Weevil herbivory and the associated reduction in recruitment increased the risk of extinction ($P_e \geqslant 5\%$ in 13 yr, 50% at 18 yr, and 100% in 43 yr, Fig. 4).

The MIHI population similarly is not viable; it surpasses the 5% risk of extinction in less than 100 yr in our simulations. The probability of extinction in populations of *C. pitcheri* at MIHI is projected to be greater than 5% (6.7%) in 8 yr and 100% in more than 500 yr under current field conditions. MIHI also was severely impacted by reductions in fecundity from simulated weevil depredation. As to be expected, both populations show a higher risk of extinction with additional and greater threats to fecundity (finch predation, inbreeding, succession, and their combination).

We also compared the larger, northern WSP population with the smaller, southern MIHI site to ask how reductions in fecundity from any factor can impact the rate of population growth (λ) (Fig. 5) following the methodology in Knight et al. (2011). This modeling began with an average matrix for each of the two populations, calculated in **popbio** package of R. We then used **poptools** in Excel 2010 to estimate declines in population growth rates with incremental decreases in fecundity. Although the southern Miller Dunes population has a population trajectory near replacement (Table 1), the rate of its decline in λ eventually surpasses that of the larger, northern WSP with extreme decreases in fecundity, probably due to the MIHI small population size.

4. Discussion

4.1. The impacts of the weevil and other threats on Pitcher's thistle

The introduced biocontrol weevil, *L. planus*, has the ability to reduce the population growth rate (and viability) of *C. pitcheri* by approximately 10.1–12% (WSP and MIHI, respectively), values similar to that reported for associated projections for the impact of *R. conicus* on *C. pitcheri* (12–15%; Louda et al., 2005). Our projected rates of population growth for Pitcher's thistle with *Larinus* seed predation at Wilderness State Park in northern Michigan ($\lambda_S = 0.8255$) and at Indiana Dunes National Lakeshore at the

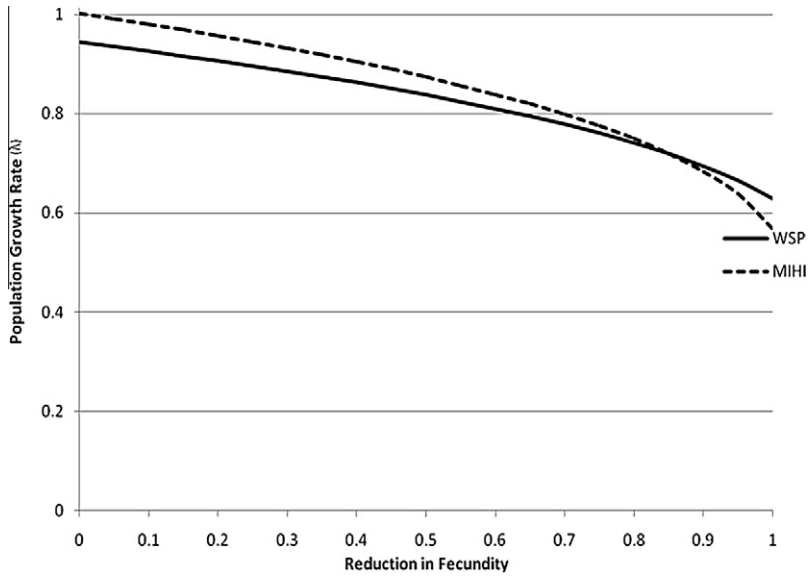

Fig. 5. A comparison of the decline in population growth rate (λ) for *Cirsium pitcheri* as a function of reductions in fecundity for two populations of *Cirsium pitcheri* in Michigan (WSP) and Indiana (MIHI). Note $\lambda = 1$ for a stable population size.

southern end of the plant's range ($\lambda_S = 0.8561$) are very similar to those of Louda et al. (2005) for simulated *Rhinocyllus* depredation on *C. pitcheri* using demographic data from uninfested populations at Sleeping Bear Dunes, MI ($\lambda = 0.8395$–0.8686). We concur with Louda et al. (2005) that this seemingly modest reduction in population growth has the ability to further push this already imperiled species towards extinction. We want to emphasize that this reduction of λ was modeled by a conservative estimate of herbivory based on observations of an early infestation at Whitefish Dunes State Park in Wisconsin (50% reduction in fecundity). Reports of *Larinus* herbivory in native thistles are few; however, *R. conicus* can reduce *Cirsium* seed output by 86% (Louda et al., 1997). Depredation by *Rhinocyllus* on native thistles increased sharply in as little as 4 yr (Louda et al., 1997).

While none of the eight populations we have studied are currently subject to all threats we model here (*Larinus* or *Rhinocyllus* weevils, inbreeding, seed predation by goldfinches, natural succession, and invasive plants), all populations are exposed to at least one and often more. The combination of natural factors such as succession, small population genetics, and predation by natives, coupled with human disturbance and impacts from exotic taxa, can severely impact the smaller populations of Pitcher's thistle which are already imperiled. While shading and litter accumulation associated with natural succession can reduce Pitcher's thistle recruitment by as much as 40% (Jolls et al., in preparation), inbreeding and seed depredation can have more serious effects on population growth (75% vs. 50–95% reduction in fecundity). At Wilderness State Park, MI, the triple threat of inbreeding and seed depredation by both native goldfinches and exotic weevils could potentially reduce recruitment by more than 98%. Effects would be more damaging for smaller populations like MIHI in IN and others at the southern end of the species range. These reductions in seed production and seedling establishment can push the population to values of lambda below anything we have observed in nature and far below a stable population structure of $\lambda = 1$. The impact of weevils and herbivores may be particularly severe for small, isolated populations of *C. pitcheri* due to Allee effects, as suggested for leaf damage of vegetative plants (Girdler and Radtke, 2006). The spread of *L. planus* and *R. conicus* appear to be from south and west (Rose et al., 2005; Bradley, 2007). The smaller, southern populations may be infested first and weevil migration could then imperil Michigan populations, where the majority of Pitcher's thistle populations occur (USFWS, 2002). Global climate change models also suggest suitable habitat for *C. pitcheri* will be limited to the northern end of the current range in the future, reinforcing the importance of the northern Michigan populations (Vitt et al., 2010).

Control of *L. planus* cannot occur too soon, given its rapid infestation of populations in Door County, WI. More vigilant monitoring for both *L. planus* and *R. conicus* are also called for in non-infested populations of *C. pitcheri*. Reports of the occurrence of *Larinus* on non-target *Cirsium* spp. are few, however, those of *Rhinocyllus* are extensive and increasing (Table 3). *Rhinocyllus* was introduced as early as 1975 in Wisconsin for control of its "preferred host", musk thistle (*Carduus nutans*). Rates of range expansion of *Rhinocyllus* have been estimated at 3.14 km/yr, as this agent spreads from the Wisconsin release sites (Bradley, 2007). Although it was hoped that control of the preferred host, musk thistle, could protect Pitcher's thistle, *Rhinocyllus* was detected in Illinois in a common garden at Chicago Botanic Garden (Havens, Personal observation), as well as on musk thistle within approximately 10 km of restored populations of *C. pitcheri* as early as 2007 (Bell, Personal communication). *Rhinocyllus* and *Larinus* also threaten other rare native thistle species (Louda and O'Brien, 2002).

Louda and her colleagues have amassed extensive evidence that many previous feeding and oviposition tests significantly underestimated the risk of these biocontrol weevils to native thistles, including *C. pitcheri*. Ironically and tragically, *Larinus* is not an effective biocontrol agent for Canada thistle (Louda and O'Brien, 2002; Reed et al., 2006) because it prefers dry, course textured sites rather than the wet seeps of *C. arvense*, a phenomenon also noted in some technical reports. Although adventive and not deliberately introduced to North America, *L. planus* has been redistributed in four Canadian western provinces and by five national agencies for Canada thistle control in the western US (Louda and O'Brien, 2002). Along with *R. conicus*, *Larinus* is actively promoted by some sites and available for purchase online. Although *Larinus* is now prohibited from interstate transport by APHIS, populations occur naturally on the eastern and western seaboards of the US (Sullivan, 2004).

Control of seed weevils in related economic species (e.g., cultivated sunflowers) offers little to no insight for control of *Larinus*

Table 3
The occurrence of biocontrol seed weevils, *Larinus planus* and *Rhinocyllus conicus*, on native and non-native *Cirsium* species in field-caged or naturally-occurring plants (from Louda et al., 1997, 2005; Gassmann and Louda, 2001; Louda and O'Brien, 2002; Wiggins et al., 2010).

Thistle species	*Larinus planus*	*Rhinocyllus conicus*
Native		
C. brevistylum		Dodge (2005)
C. calcareum		Dodge (2005)
C. callilepis		Dodge (2005)
C. canescens		Louda et al. (1997)
C. canovirens		Dodge (2005)
C. carolinianum		Wiggins et al. (2010)
C. ciliolatum		Wiggins et al. (2010)
C. eatonii		Dodge (2005)
C. flodmanii	Dodge (2005), Rees (1977, 1978) and Zwölfer and Harris (1984)	Dodge (2005)
C. fontinale		Wiggins et al. (2010)
C. hillii		Sauer and Bradley (2008)
C. hydrophilium var. *vaseyi*		Herr (2004)
C. neomexicanum		Dodge (2005)
C. occidentale		Palmisano and Fox (1997) and Dodge (2005)
C. ochrocentrum		Dodge (2005)
C. peckii		Dodge (2005)
C. perplexans	Dodge (2005)	Dodge (2005)
C. pitcheri	This study	In IL common garden, this study
C. scariosum		Dodge (2005)
C. scopulorum		Dodge (2005)
C. subniveum		Dodge (2005)
C. tweedy		Louda et al. (1997)
C. undulatum var. *tracyi*	Louda and O'Brien (2002) and Dodge (2005)	
C. undulatum var. *undulatum*	Dodge (2005)	Rees (1977, 1978) and Zwölfer and Harris (1984)
Non-native		
C. arvense		Louda et al. (1997)
C. centaureae		Louda et al. (1997)
C. nutans		Louda et al. (1997)
C. vulgare		Laing and Heels (1978) cf. Gassmann and Louda (2001)

and *Rhinocyllus*. To date, other controls for red sunflower seed weevil adults (*Smicronyx fulvus* LeConte) in economically important Asteraceae (pheromone or plant volatiles traps, resistant germplasm) are not promising (Roseland et al., 1992). Possible chemical controls come with their own risks; many are EPA restricted-use pesticides (e.g., Furadan 4F, Oseto and Burr, 1990). Protection of seed output and seedling success is key to *C. pitcheri* population viability (Jolls et al., Unpublished results). The most useful protection may be very labor-intensive netting of flowering heads to exclude seed weevils during oviposition, yet not to the exclusion of visiting pollinators (McEachern and Pavlovic, Unpublished results). Such efforts will require extensive knowledge of seed predation phenology and life history as well as *C. pitcheri* pollination biology and may even require coupling netting with hand-pollination if oviposition timing and pollination completely overlap.

Threats from biocontrol agent(s) must be put into management and conservation context for *C. pitcheri*. Prior to its USFWS 5-Year Recovery Review, Pitcher's thistle was listed as "8C", denoting moderate threat, a high degree of recovery, and a "high degree of conflict with development and other forms of economic activity" (USFWS, 2010). Pitcher's thistle may not respond quickly to positive effects of management yet will decline quickly to extinction from seed predators. Repeated failure of seed set from weevil predation leaves only vegetative individuals which live no more than 12 yr. *C. pitcheri* is a relatively long-lived monocarp whose habitat is coupled with lake levels that change with 5–10 and even 150-yr periodicity. Long-lived plant species can be slow to respond to environmental change (Colling and Matthies, 2006). *C. pitcheri* has been part of the shoreline landscape only since the Pleistocene retreat of glacial Lake Nipissing (4000 YBP). This thistle species is dependent on large-scale spatial association as a metapopulation (McEachern et al., 1994) and long-term temporal association with environmental disturbance. Our study populations, both natural and restored, are fluctuating asynchronously with respect to seedling production and recruitment. This asynchrony suggests that additional factors, such as demography and genetics, affect *C. pitcheri* populations differently and that populations differ in their ability to recover from threats (Fant et al., Unpublished results). Nearly two decades after reintroduction, it is yet unclear whether restored populations are viable (Bell, Personal communication). While restored Pitcher's thistle populations may appear to be successful in the short-term, given $\lambda \geqslant 1.0$; the majority of natural populations are below replacement (Jolls et al., Unpublished results). Of the five natural populations for which we have long-term monitoring data (3–21 yr), none have positive population growth rates (all $\lambda_S < 1.0$), suggesting these populations are not viable during the long-term. Seed loss from this invasive biocontrol agent could well be what tips the balance for *C. pitcheri* toward extinction.

4.2. Use of biocontrol: a cautionary tale

Our work adds to a limited but increasing body of knowledge on quantification of the population-level impacts of insect herbivory on rare plants (Ancheta and Heard, 2011). Although some biological control agents may benefit some rare plant taxa (Meyer and Fourdrigniez, 2011), the negative impacts of both native insects and introduced herbivores are well-documented, including from the introduced biocontrol, *R. conicus* on native thistles (Turner et al., 1987; Gassmann and Louda, 2001, Table 3). The USFWS Pitcher's thistle Recovery Plan (USFWS, 2002) also reports threats to *C. pitcheri* from *Rhinocyllus*, given reports in other native thistles (Goeden and Ricker, 1986a,b, 1987a,b). Unfortunately, we now add *Larinus planus* to the list. Louda and O'Brien (2002) were the first to call for cessation of the deliberate spread of *L. planus* and that "compelling evidence should be required that no other risks exist for rare species before releases are restarted" (p. 725). Other congeners, *L. curtus*, *L. minutus* and *L. obtusus*, have been released and

promoted in British Columbia and the United States for control of invasive knapweeds (*Centaurea maculosa* and *Centaurea diffusa*) and yellow starthistle (*Centaurea solstitialis*). Still other agents are potential risks to *C. pitcheri* and other native thistles. Dodge (2005) reports that at least 11 insects and two fungi have been introduced or redistributed to control plants in the subtribe *Carduinae* (Gassmann and Kok, 2002; Kok and Gassmann, 2002; McClay et al., 2002; Table 3).

5. Conclusions

Currently none of the eight populations we have studied are subject to all of the threats modeled here (weevils, inbreeding, seed predation by goldfinches, natural succession, and invasive plants), but all populations are exposed to at least one or more. This argues for long-term seed storage for this monocarpic perennial as well as vigilant monitoring for threats and immediate active management to control them when found. Control of invasive vegetation such as spotted knapweed and baby's breath have been successful using hand-pulling, herbicide application, and severing of the caudex with hand axes (Loope et al., 1995). Our report of *L. planus* and its impact on Pitcher's thistle population viability confirms USFWS 5-Year Review recommendations that there be no change in classification of this federally threatened species. If anything, our projections of the effects of biocontrol weevils and other emerging threats coupled with documented decreases in population sizes at the southern and western extremes of the range (McEachern, Unpublished data), argue for an uplisting for *Cirsium pitcheri* from threatened to endangered.

Acknowledgements

The authors thank Elizabeth Brackin, Michelle Boyle, Ariel Campbell, Kristin Cribb, Noura Hamzé, Samara Hamzé, Jill Johnston, Lisa Keller, Erica Kociolek, Lindsay Leverett, Tiffany Lin, Christa Lutzke, Greg Nozko, Sally Oviatt, Noel Pavlovic, Callie Pflafkin, Bob Pillsbury, C. Smith, Amalia Spankowski, Shannon Still, Julie Stumpf, Melissa Tienes, D. Trexel-Kroll, Kristin Uthus, Alison Varty, and Eric Young for assistance in the field. We thank Tim Bell, Marlin Bowles, and Jeremie Fant for sharing unpublished data. The manuscript was improved by comments from Richard Primack, Ed Guerrant, and an anonymous reviewer. We thank Emily Yates for creating Fig. 1. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. This research was supported by NSF award DEB 0516058 to K. Havens, T. Bell, M. Bowles, C. Jolls, and K. McEachern. Additional support came from the Michigan Department of Natural Resources, U.S. Geological Survey, and University of Michigan Biological Station. The funding sources had no role in study design, data collection, analysis or interpretation.

References

Ancheta, J., Heard, S.B., 2011. Impacts of insect herbivores on rare plant populations. Biol. Conserv. 144, 2395–2402. http://dx.doi.org/10.1016/j.biocon.2011.06.019.

Baskett, C.A., Emery, S.M., Rudgers, J.A., 2011. Pollinator visits to threatened species are restored following invasive plant removal. Int. J. Plant Sci. 172, 411–422.

Bell, T.J., Bowles, M.L., McEachern, A.K., 2003. Projecting the success of plant population restoration with viability analysis. In: Brigham, C.A., Schwartz, M.W. (Eds.), Population Viability in Plants. Springer, Berlin, pp. 313–350.

Bevill, R.L., Louda, S.M., Stanforth, L.M., 1999. Protection from natural enemies in managing rare plant species. Conserv. Biol. 13, 1323–1331. http://dx.doi.org/10.1046/j.1523-1739.1999.98450.x.

Bowles, M.L., McBride, J.L., 1996. Status and structure of a Pitcher's thistle (*Cirsium pitcheri*) population reintroduction to Illinois Beach Nature Preserve. In: Falk, D.A., Millar, C.I., Olwell, M. (Eds.), Restoring Diversity: Ecological Restoration and Endangered Plants. Island Press, New York, pp. 423–431.

Bradley, K.L., 2007. Quantifying the spatial distribution, abundance, and host use of the invasive insect, *Rhinocyllus conicus*, across Wisconsin and the greater Chicago area. Report to the Bureau of Endangered Resources, Wisconsin Department of Natural Resources. Unpublished Report, p. 32. (cf. USFWS Five Year Review).

Caswell, H., 2001. Matrix Population Models. Construction, Analysis, and Interpretation. Sinauer Associates, Sunderland, Massachusetts, p. 722.

Colling, G., Matthies, D., 2006. Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). J. Ecol. 94, 959–972.

Cripps, M.G., Gassman, A., Fowler, S.V., Bourdôt, McClay, A.S., Edwards, G.R., 2011. Classical biological control of *Cirsium arvense*: lessons from the past. Biol. Control 57, 165–174.

Dodge, G.J., 2005. Ecological Effects of the Biocontrol Insects, *Larinus planus* and *Rhinocyllus conicus*, on Native Thistles, Unpublished PhD Thesis, University of Maryland, College Park, Maryland, p. 187.

D'Ulisse, A., Maun, M.A., 1996. Population ecology of *Cirsium pitcheri* on Lake Huron sand dunes: II. Survivorship of plants. Can. J. Bot. 74, 1701–1707.

Fant, J.B., Havens, K., Keller, J.M., Radosavljevic, A., Yates, E.D., Glacial migration, biogeography and genetics of a narrow endemic thistle, *Cirsium pitcheri* (Asteraceae). American Journal of Botany, in preparation.

Gassmann, A., Kok, L.T., 2002. Musk thistle (nodding thistle). In: van Driesche, R., Blossey, B., Hoddle, M., Lyon, S., Reardon, R. (Eds.), Biological Control of Invasive Plants in the Eastern United States. USDA Forest Service, Morgantown, West Virginia, pp. 229–245.

Gassmann, A., Louda, S.M., 2001. *Rhinocyllus conicus*: initial evaluation and subsequent ecological impacts in North America. In: Wajnberg, E., Scott, J.K., Quimby, P.C. (Eds.), Evaluating Indirect Ecological Effects of Biological Control. CABI Science Publishing, United Kingdom, pp. 147–183.

Girdler, E.B., Radtke, T.A., 2006. Conservation implications of individual scale spatial pattern in the threatened dune thistle, *Cirsium pitcheri*. Am. Midl. Nat. 156, 213–228. http://dx.doi.org/10.1674/0003-0031(2006) 156[213:CIOISS]2.0.CO;2.

Goeden, R.D., Ricker, D.W., 1986a. Phytophagous insect faunas of two introduced *Cirsium* thistles, *C. ochrocentrum*, and *C. vulgare*, in southern California. Ann. Entomol. Soc. Am. 79, 945–952.

Goeden, R.D., Ricker, D.W., 1986b. Phytophagous insect faunas of the two most common native *Cirsium* thistles, *C. californicum* and *C. proteanum*, in southern California. Ann. Entomol. Soc. Am. 79, 953–962.

Goeden, R.D., Ricker, D.W., 1987a. Phytophagous insect faunas of the native thistles, *Cirsium brevistylum*, *Cirsium congdonii*, *Cirsium occidentale*, and *Cirsium tioganum* in southern California. Ann. Entomol. Soc. Am. 0, 152–160.

Goeden, R.D., Ricker, D.W., 1987b. Phytophagous insect faunas of native *Cirsium* thistles, *C. mohavense*, *C. neomexicanum*, and *C. nidulum*, in the Mojave Desert of southern California. Ann. Entomol. Soc. Am. 80, 161–175.

Hamzé, S.I., 1998. Population Demography and Seed and Seedling Ecology of the Great Lakes Endemic Pitcher's Thistle (*Cirsium pitcheri*, Asteraceae), Unpublished Master's Thesis. East Carolina University, Greenville, North Carolina, p. 114.

Hamzé, S.I., Jolls, C.L., 2000. Germination ecology of a federally threatened endemic thistle, *Cirsium pitcheri*, of the Great Lakes. Am. Midl. Nat. 143, 141–153. http://dx.doi.org/10.1674/0003-0031(2000) 143.

Herr, J.C., 2004. Non-target Impact of the Weed Biocontrol agent *Rhinocyllus conicus* on Rare Native California Thistles in the Genus *Cirsium*. Unpublished PhD Dissertation, University of California, Berkeley, California, p. 109.

Jolls, C.L., Marik, J.E., Hamzé, S.I., Population viability analysis and the effects of light availability and litter on populations of *Cirsium pitcheri*, a rare, monocarpic perennial. Botany, in preparation.

Kok, L.T., Gassmann, A., 2002. Plumeless thistle (curled thistle, bristly thistle). In: van Driesche, R., Blossey, B., Hoddle, M., Lyon, S., Reardon, R. (Eds.), Biological Control of Invasive Plants in the Eastern United States. USDA Forest Service, Morgantown, West Virginia, pp. 255–261.

Knight, T.M., Havens, K., Vitt, P., 2011. Will the use of less fecund cultivars reduce the invasiveness of perennial plants? Bioscience 61, 816–822.

Laing, J.E., Heels, P.R., 1978. Establishment of an introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) for the biological control of nodding thistle (Compositae) in southern Ontario. Proc. Entomol. Soc. Ont. 109, 3–8 (cf. Gassman and Louda, 2001).

Leege, L.M., Murphy, P.G., 2001. Ecological effects of the non-native *Pinus nigra* on sand dune communities. Can. J. Bot. 79, 429–437.

Loope, W.L., Siterlet, C.L., McKenna, A.P., 1995. Distribution and Experimental Management of *Gypsophila paniculata* (baby's breath) Within Sleeping Bear Dunes National Lakeshore, Phase I. Initial Assessment and Plot Establishment, Summer 1995. Sleeping Bear Dunes National Lakeshore, Empire, Michigan.

Louda, S.M., Kendall, D., Connor, J., Simberloff, D., 1997. Ecological effects of an insect introduced for the biological control of weeds. Science 277, 1088–1090.

Louda, S.M., O'Brien, C.W., 2002. Unexpected ecological effects of distributing the exotic weevil, *Larinus planus* (F.), for the biological control of Canada thistle. Conserv. Biol. 16, 717–727.

Louda, S.M., Pemberton, R.W., Johnson, M.T., Follett, P.A., 2003. Nontarget effects: the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annu. Rev. Entomol. 48, 365–396.

Louda, S.M., Rand, T.A., Arnett, A.E., McClay, A.S., Shea, K., McEachern, K., 2005. Evaluation of ecological risk to populations of a threatened plant from and invasive biocontrol insect. Ecol. Appl. 15, 234–249.

Loveless, M.D., 1984. Population Biology and Genetic Organization in *Cirsium pitcheri*, an Endemic Thistle, Unpublished PhD Dissertation, University of Kansas, Lawrence, Kansas, p. 109.

Marik, J.E., 2007. Population Viability Analysis and Restoration Ecology of a Federally Threatened Thistle of the Great Lakes, *Cirsium pitcheri*. Unpublished MS Thesis, East Carolina University, Greenville, North Carolina, p. 81.

McClay, A.S., Bourchier, R.S., Butts, R.A., Peschken, D.P., 2002. *Cirsium arvense* (L.) Scopoli, Canada thistle (Asteraceae). In: Mason, P.G., Huber, J.T. (Eds.), Biological Control Programmes in Canada, 1981–2000. CABI Publishing, New York, pp. 318–330.

McEachern, A.K., 1992. Disturbance Dynamics of Pitcher's thistle (*Cirsium pitcheri*) Populations in Great Lakes Sand Dune Landscapes. Unpublished PhD Dissertation, University of Wisconsin-Madison, Madison, Wisconsin, p. 238.

McEachern, K., Bowles, M., Pavlovic, N., 1994. A metapopulation approach to Pitcher's thistle (*Cirsium pitcheri*) recovery in southern Lake Michigan dunes. In: Bowles, M., Whelen, C. (Eds.), Restoration of Endangered Species. Cambridge University Press, Cambridge, Massachusetts, pp. 194–218.

Menges, E.S., 1990. Population viability analysis for an endangered plant. Conserv. Biol. 4, 52–62.

Meyer, J., Fourdrigniez, M., 2011. Conservation benefits of biological control: the recovery of a threatened plant subsequent to the introduction of a pathogen to contain an invasive tree species. Biol. Conserv. 144, 106–113. http://dx.doi.org/10.1016/j.biocon.2010.08.004.

Morris, W.F., Doak, D.F., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, Massachusetts, p. 480.

Oseto, C.Y., Burr, W.R., 1990. Timing insecticide applications for control of the red sunflower seed weevil (Coleoptera: Curculionidae) on cultivated sunflower. J. Agric. Entomol. 7, 337–341.

Pellerin, S., Huot, J., Côté, S., 2006. Long term effects of deer browsing and trampling on the vegetation of peatlands. Biol. Conserv. 128, 316–326.

Palmisano, S., Fox, L.R., 1997. Effects of mammal and insect herbivory on population dynamics of a native Californian thistle, *Cirsium occidentale*. Oecologia 111, 413–421.

Reed, C.C., Larson, D.L., Larson, J.L., 2006. Canada thistle biological control agents on two South Dakota wildlife refuges. Nat. Areas J. 26, 47–52.

Rees, N.E., 1977. Impact of *Rhinocyllus conicus* on thistles in southwestern Montana. Environ. Entomol. 6, 839–842 (cf. Wiggins et al., 2010).

Rees, N., 1978. Interactions of *Rhinocyllus conicus* and thistles in the Gallatin valley. In: Frick, K.E. (Ed.), Biological Control of Thistles in the Genus *Carduus* in the United States: A Progress Report. Science and Education Administration. US Department of Agriculture, New Orleans, Louisiana, pp. 31–38 (cf. Wiggins et al., 2010).

Rose, K.E., Rees, M., Louda, S.M., 2005. Demographic and evolutionary impacts of native and invasive insect herbivores: a case study with Platte thistle, *Cirsium canescens*. Ecology 86, 453–465.

Roseland, C.R., Bates, M.B., Carlson, R.B., Oseto, C.Y., 1992. Discrimination of sunflower volatiles by the red sunflower seed weevil. Entomol. Exp. Appl. 62, 99–106. 410350032,12,1.

Sauer, S.A., Bradley, K.L., 2008. First record for the biological control agent *Rhinocyllus conicus* (Coleoptera: Curculionidae) in a threatened native thistle, *Cirsium hillii* (Asteraceae), in Wisconsin, USA. Entomol. News 119, 90–95. http://dx.doi.org/10.3157/0013-872X [90:FRFTBC]2.0.CO;2.

Stanforth, L.M., Louda, S.M., Bevill, R.L., 1997. Insect herbivory on juveniles of a threatened plant, *Cirsium pitcheri*, in relation to plant size, density and distribution. Ecoscience 4, 57–66.

Stubben, C., Milligan, B., 2007. Estimating and analyzing demographic models using the **popbio** package in R. J. Stat. Softw. 22, 1–23.

Sullivan, P.G., 2004. Thistle Control Alternative. Pest Management Current Topic. ATTRA, National Sustainable Agricultural Information Service. <http://www.attra.ncat.org/attra-pub/thistlecontrol.html>.

Tuljapurkar, S.D., 1982. Population-dynamics in variable environments. 3. Evolutionary dynamics of r-selection. Theor. Popul. Biol. 21, 141–165.

Turner, C.E., Pemberton, R.W., Rosenthal, S.S., 1987. Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera, Curculionidae) in California. Environ. Entomol. 16, 111–115.

US Fish and Wildlife Service, 1988. Endangered and threatened wildlife and plants: determination of threatened status for *Cirsium pitcheri*. Federal Register 53(137), 27137–27141.

US Fish and Wildlife Service, 2002. Pitcher's Thistle (*Cirsium pitcheri*) Recovery Plan. Fort Snelling, Minnesota, p. 92.

US Fish and Wildlife Service, 2010. Pitcher's Thistle (*Cirsium pitcheri*) 5-Year Review: Summary and Evaluation. US Fish and Wildlife Service, Midwest Region, East Lansing Field Office, East Lansing, Michigan, p. 29.

Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. Biol. Conserv. 143, 18–27.

Wheeler Jr., A.G., Whitehead, D.R., 1985. *Larinus planus* (F.) in North America (Coleoptera: Curculionidae: Cleoninae) and comments on biological control of Canada thistle. Proc. Entomol. Soc. Wash. 87, 751–758.

White, J.C., 1972. A European weevil, *Larinus carlinae* Oliver, collected in Maryland. Coop. Econ. Insect Rep. 22, 418.

Wiggins, G.J., Grant, J.F., Lambdin, P.L., Ranney, J.W., Wilkerson, J.B., Reed, A., Follum, R.A., 2010. Host utilization of field-caged native and introduced thistle species by *Rhinocyllus conicus*. Environ. Entomol. 39, 1858–1865. http://dx.doi.org/10.1603/EN10053.

Zwölfer, H., Harris, P., 1984. Biology and host specificity of *Rhinocyllus conicus* (Froel.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans* L. J. Appl. Entomol. 97, 36–62 (cf. Wiggins et al., 2010).