

5-2015

# Rareness Starts Early for Disturbance-Dependent Grassland Plant Species

Matthew Candeias

SUNY Buffalo State, [candeim01@mail.buffalostate.edu](mailto:candeim01@mail.buffalostate.edu)

## **Advisor**

Robert J. Warren II, Ph.D., Assistant Professor of Biology

## **First Reader**

Robert J. Warren II, Ph.D., Assistant Professor of Biology

## **Second Reader**

Daniel Potts, Ph.D., Associate Professor of Biology

## **Third Reader**

Amy McMillan, Ph.D., Associate Professor of Biology

## **Department Chair**

I. Martha Skerrett, Chair and Associate Professor of Biology

To learn more about the Biology Department and its educational programs, research, and resources, go to <http://biology.buffalostate.edu/>.

---

## Recommended Citation

Candeias, Matthew, "Rareness Starts Early for Disturbance-Dependent Grassland Plant Species" (2015). *Biology Theses*. 14.  
[http://digitalcommons.buffalostate.edu/biology\\_theses/14](http://digitalcommons.buffalostate.edu/biology_theses/14)

Follow this and additional works at: [http://digitalcommons.buffalostate.edu/biology\\_theses](http://digitalcommons.buffalostate.edu/biology_theses)

 Part of the [Other Ecology and Evolutionary Biology Commons](#)

**Rareness starts early for disturbance-dependent grassland plant species**

by

**Matthew Candeias**

**An Abstract for a Thesis in  
Biology**

**Submitted in Partial Fulfillment  
of the Requirements  
for the Degree of**

**Master of Arts**

**May 2015**

**Buffalo State College  
State University of New York  
Department of Biology**

## **ABSTRACT OF THESIS**

Rareness starts early for disturbance-dependent grassland plant species

Ecological communities always contain a few common species and an abundance of rare species. Mechanisms determining commonness and rarity require experimental investigation. Given that most plant mortality occurs in seeds and seedlings, recruitment best predicts plant community assemblage and distributions. In northeastern North America, grassland plant species constitute a sizable portion of the native flora. Approximately 30% of western New York's threatened and endangered flora are associated with grasslands, apparent leftovers from a post-glacial landscape. I investigated the mechanisms behind grassland species commonness and rarity by examining how habitat type, disturbance and biotic interactions limit seed recruitment for three rare grassland species and their common congeners. If grassland species rarity is determined by habitat suitability, then the rare grassland species will be more responsive to habitat heterogeneity and manipulation than are the common species. Rare species successfully recruited where burning reduced initial competitor density, but otherwise appeared severely limited by interspecific competition. Because both the rare and common plant species survived equally well in the forest and edge habitats, but only common plant species did much better in the meadows, the competition for space may be the limiting factor for rare grassland plants. Pollinator limitation may explain grassland plant rarity for one of the study species, which suggests that small populations may be limited by a lack of pollinator visits. Commonness and rarity are temporal designations that can change as disturbance alters the landscape. The results of this experiment suggest that for rare grassland plants, widespread burning and planting appears to be required, both to create suitable habitat and encourage positive biotic interactions.

**Rareness starts early for disturbance-dependent grassland plant species**

by

**Matthew Candeias**

**A Thesis  
in  
Biology**

**Submitted in Partial Fulfillment  
of the Requirements  
for the Degree of**

**Master of Arts**

**May 2015**

**Approved by:**

**Robert J. Warren II, Ph.D.  
Assistant Professor  
Chairperson of the Committee  
Thesis Adviser**

**I. Martha Skerrett, Ph.D.  
Associate Professor and Chair  
Department of Biology**

**Kevin Railey, Ph.D.  
Associate Provost and Dean  
The Graduate School**

THESIS COMMITTEE

Robert J. Warren II, Ph.D.  
Assistant Professor of Biology

Daniel Potts, Ph.D.  
Associate Professor of Biology

Amy McMillan, Ph.D.  
Associate Professor of Biology

## ACKNOWLEDGEMENTS

I would first and foremost like to thank my thesis adviser Dr. Robert J. Warren II. Your expertise and guidance was invaluable throughout this entire process. You represent the kind of ecologist that I aspire to become.

I would also like to thank my committee members, Dr. Daniel Potts and Dr. Amy McMillan. Your guidance and input over the last two years has opened up so many new avenues of research. I appreciate your cooperative insights and dedication to making this project scientifically sound.

A special thanks goes to Sue Chislett. You have saved me numerous times over the past two years. Your willingness to go above and beyond to help confused grad students is a testament to the fact that the Biology Department simply could not function without you. Thank you so very much.

To all of my lab mates as well as those who helped during a hot and humid field season, thank you dearly. This project went smoothly because of you and the hours we put in together. You are wonderful friends.

To my ever supportive parents, this journey began long before I even knew what ecology was. Your dedication, support, and love over these last 27 years has shaped me into the person I am today. I could not have done any of this without you.

Finally, I would like to thank Sara Johnson for both putting up with me during times of stress and for helping me every step of the way. If it wasn't for you strapping a flashlight to your head and planting seeds well into the night I don't think this project would have gotten off the ground as smoothly as it did. You kept me sane and focused and I am forever grateful for your love and support. Thank you.

## TABLE OF CONTENTS

List of tables.....	7
List of figures.....	8
Introduction.....	10
Methods.....	15
Study Site.....	15
Study species.....	16
Seed Establishment Design.....	17
Pollinator Observation Sites.....	18
Pollinator Observation Design.....	19
Data Analysis.....	20
Results.....	21
Seedling Establishment Experiments.....	21
Pollinator Observation.....	23
Discussion.....	23
References.....	27
Tables.....	38
Figures.....	42

## LIST OF TABLES

Table 1. State ranking system for plant status in New York

Table 2. Abiotic differences between habitats



## LIST OF FIGURES

Fig. 1 – Treatment grid design for experimental burning (burn) and herbivore exclusion (exclusion).

Figure 2. Mean ( $\pm$  SE) % germination for rare (white) and common (gray) grassland species. Means with different letters are significantly different.

Figure 3. Treatment interaction plot showing mean ( $\pm$ SE) % germination across experimental treatments. Rare species germination was significantly higher than common species in the burn treatments whereas common species germination was significantly higher than rare in the enclosure treatments. Both rare and common species germination was higher in treatments that included burning.

Figure 4. Mean ( $\pm$ SE) % survival for rare (white) and common (gray) species. There was no statistically significant difference in species survival, but none of the *Agastache nepetoides* plants survived

Figure 5. Habitat interaction plot showing mean ( $\pm$ SE) % survival. Both rare and common species survived equally poorly in edge habitat and equally better in forest habitat, but the common species survived significantly better in the meadow habitat than the rare species.

Figure 6. Quantile regression indicating that interspecific biomass set the upper limits on rare species germination (A) but not common species germination (B) at the 99<sup>th</sup> quantile.

Figure 8. Mean ( $\pm$ SE) pollinator visitation per flower for rare (white) and common (gray) grassland species. Visitation was significantly greater for *Eupatorium perfoliatum* than *Liatris cylindracea* (A) but did not differ between *Symphiotrichum oolentangiensis* and *Symphiotrichum novae-angliae* (B).

## **Introduction:**

Ecological communities always contain a few common species and lots of uncommon ones (Preston 1948, Whittaker 1965, Bevill and Louda 1999, McGill et al. 2007). However, what determines commonness and rarity remains an open question (Hubbell 2001, Warren et al. 2011). Plant distributions suggest that habitat generalists are common and specialists are rare (Wamelink et al. 2014, Partel et al. 2005), but these inferences do not indicate the mechanisms causing the patterning (Partel et al. 2005; and references therein). Conversely, comparing and contrasting plant traits between rare and common species has not revealed any clear correlations between specific traits and abundance (Bevill & Louda 1999, Murray et al. 2002). Given that most plant mortality occurs in seeds and seedlings (Fenner and Kitajima 1999, Harper 1977), commonness and rarity in plant communities may begin with recruitment (Grubb 1977, Albrecht and McCarthy 2009, Moore 2009, Warren and Bradford 2011).

Recruitment (seed and seedling survival) is essential for the survival and persistence of plant populations (Eriksson & Ehrlén 1992). Individual plants must replace themselves within each generation to maintain populations in occupied habitat, or they must establish new populations by dispersing propagules to novel habitats. For plants, mortality is highest during the transition from seed to juvenile, making recruitment a bottleneck through which populations must successfully pass for persistence (Chambers & MacMahon 1994, Fenner 2000, Clark et al. 2007). Whereas recruitment failure in unsuitable habitat hinders colonization, plants also can be seed limited in optimal habitat (Eriksson & Ehrlén 1992, Verheyen & Hermy 2004). As such, early life-history events (e.g. dispersal, germination, seedling survival) set the stage for plant community patterning in space and time (Clark 1996, Warren & Bradford 2011). Plant rarity might then be explained by habitat limitation (seeds in unsuitable habitat), seed limitation (no

seeds in suitable habitat) or a combination of both (Eriksson & Ehrlén 1992, Nathan & Muller-Landau 2000, Turnbull et al. 2000, Clark et al. 2007).

Dispersal limitation can leave suitable habitat unoccupied (Pulliam 2000) as evidenced by successful experimental introduction of plants into novel habitats (Eriksson & Ehrlén 1992, Primack & Miao 1992, van der Meijden et al. 1992, Crawley & Brown 1995, Ackerman et al. 1996, Clark et al. 1998, Coulson et al. 2001, Clark et al. 2007, Piqueray et al. 2013). Even at local scales, some plant species are dispersal limited just 100 m from large natural populations, showing that even modest distances can form dispersal barriers (Verheyen & Hermy 2004). In these instances, the experimental addition of seed leads to an increase in the plant population, indicating unoccupied suitable habitat (Eriksson & Ehrlén 1992, Primack & Miao 1992, van der Meijden et al. 1992, Crawley & Brown 1995, Ackerman et al. 1996, Clark et al. 1998, Coulson et al. 2001, Clark et al. 2007, Piqueray et al. 2013).

Habitat quality also limits plant species recruitment (Clark et al. 1998, Coulson et al. 2001, Clark et al. 2007, Piqueray et al. 2013). Both biotic and abiotic conditions can make habitat unsuitable, and often species are limited by a combination of both (Coulson et al. 2001, Piqueray et al. 2013). For example, inferior resource competitors (e.g., light, nitrogen) recruit poorly in the presence of superior competitors (Tilman 1987, Zeiter et al. 2006, MacDougall & Wilson 2007). For a given resource, species often are limited by abiotic tolerance where the resource is low, whereas biotic interactions are limiting where the resource is high (Connell 1975, Warren and Bradford 2011). In conditions of high resource availability, ample seed production can lead to seed predation by granivores (Brown & Heske 1990, Howe & Brown 2000, 2001, Orrock et al. 2006). Seed predation varies among plant species (Orrock et al. 2006), and seed predators (i.e. rodents, arthropods, and birds) can considerably reduce plant abundance

for the species they feed upon (Edwards & Crawley 1999, Crawley 2000, Orrock et al. 2006). As such, seed predators can eliminate plant species before they have a chance to germinate (Orrock et al 2006). Preferential seedling herbivory also may play a significant biotic role in recruitment limitation (MacDougall & Wilson 2007). For example, white-tailed deer (*Odocoileus virginianus*) populations are at historically high densities in eastern North America (Garrot et al. 1993), and they often browse specific plant species, which cause considerable changes in plant communities (Stromayer & Warren 1997, Rooney et al. 2003). Moreover, physical disturbance caused by deer (e.g., trampling and scraping) alter microclimate conditions and may change recruitment suitability for some species (Rooney & Waller 2002).

Negative species interactions can be limiting, but failed positive interactions also render habitat unsuitable. A lack of pollinators can limit plant recruitment both by being absent and by simply overlooking small, remnant plant populations (Sih & Baltus 1987, Hennig & Ghazoul 2011, Pauw 2013). Pollinators have a high fidelity to the strongest and most abundant floral cues (Hennig & Ghazoul 2011, Ye et al. 2014). As a result, pollinators are more likely to visit large conspecific patches with abundant flowers (Sih & Baltus 1987, Hennig & Ghazoul 2011). Hence, rare plants receive fewer pollinator visits in the presence of more abundant flowering species, (Mosquin 1971, Sih & Baltus 1987, Hennig & Ghazoul 2011). For example, most of the poor pollination in *Nepeta cararia*, a species in the mint family, was explained by its small patch size (Sih & Baltus 1987). Suitable pollinators, especially some bees (*Bombus* spp.), were plentiful, but they were more likely to visit larger flower patches. Pollinator disinterest in small patches resulted in reduced seed set and thus a reduction in the potential for establishing new populations (Sih & Baltus 1987).

Abiotic habitat conditions underlay all plant distributions (Peterson et al. 2011). Most seeds simply cannot germinate everywhere. As such, rarity may also be explained by abiotic habitat specificity. For example, variation in soil texture influences how water moves through the soil – the coarser the soil, the less water will be held (Brubaker 1975, Szeicz et al. 1991). Bruno (2002) illustrated that soil texture was a critical limiting factor in the abundance of rare plant species on cobble beaches in Rhode Island. Germination for these rare plants depends on the presence of fine-grained substrate, which only accumulates when wave action is slowed. In addition to soil texture, the abundance of different nutrients such as N or P determines which species thrive. For example, elevated levels of N and P select for more competitive common species (Standish et al. 2007, Cramer et al. 2008). Such variations in resource availability correspond with increased species diversity, allowing for the coexistence of good and poor competitors, specialists and generalists (MacArthur and MacArthur 1961, Whittaker 1972, Rosenzweig 1981, 1991).

Glaciation creates large-scale habitat heterogeneity in both space and time (Pielou 1991, Ramankutty & Foley 1999, Koerner et al. 1999, Dupouey et al. 2002). Glaciers cleared vegetation cover across a wide swath of North America during the most recent glacial maximum (approximately 20,000 ya) (Pielou 1991). When the glaciers receded from northeastern North America (approximately 12,000 B.P.), large deposits of glacial sediment, devoid of plant cover were left behind. Post-glacial till generally has a thin layer of sandy soil overlaying an extensive gravel layer, which causes water to drain rapidly and making the soil vulnerable to drought (Cain et al. 1937, Hamilton 2012). Drought tolerant plants initially colonized the till after glaciers retreated and formed “prairie peninsula” communities that stretched from western to coastal New York (Gordon 1939, Hamilton 2012, York 2012). These habitats persisted for centuries due to a

combination of increased temperatures and decreased precipitation during the Holocene Epoch (Gordon 1939, York 2012). Early human land use in the northeastern United States possibly maintained grassland communities by disturbing the landscape through large-scale burning, which limits tree recruitment (Steuter 1991, Nowacki & Abrams 2008, Hamilton 2012).

However, in recent decades, prairie peninsula communities declined into disjunct populations as a result of tree colonization followed by modern land use (e.g. industrial agriculture) (Pielou 1991, Overpeck et al. 1992, Hamilton 2012). The remaining prairie peninsula communities in northeastern North America are remnants of the once extensive distribution (Hamilton 2012).

Modern large-scale, intensive agriculture has become the largest form of disturbance in the United States (Ramankutty & Foley 1999). Whereas agriculture matches glaciation in the scale of disturbance (large-scale clearing, propagule destruction and soil alteration), agricultural processes (ie. tillage and fertilization) leave a radically different legacy on soil structure and nutrient levels (Dupouey et al. 2002, Edmeades 2003, Cramer et al. 2008, Morris et al. 2013). In addition, the introduction of non-native pasture species from Europe and Asia alter the composition of surrounding plant communities, which, in turn, alters the propagule pool that arrives on recently abandoned agricultural lands (Dupouey et al. 2002). Together, these dynamics cause considerable difference in the types of plant species capable of colonizing abandoned agriculture fields by selecting for nutrient-demanding, competitive species (Dupouey et al. 2002). Such changes can be measured centuries later (Koerner et al. 1999, Dupouey et al. 2002).

Approximately 30% of rare and uncommon plants in New York are remnant prairie peninsula species (New York Natural Heritage 2013). These same species are currently more abundant in the relatively drier Midwestern (U.S.) habitats east of the Rocky Mountains where

drought and fire limit trees and shrubs (Lauenroth 1979, Steuter 1991, Nowacki & Abrams 2008, Hamilton 2012), but the absence of these factors may limit grassland remnants in northeastern N.A. Still, it is difficult to discern whether grassland species rarity in northeastern N.A. is because the landscape no longer contains sufficient suitable habitat or because they are unable to disperse from remaining small, disjunct populations. The objective of this research is to examine whether seed or habitat limitation explains rarity and commonness in remnant grassland species in western New York (WNY). I used seed addition experiments coupled with microhabitat manipulations (burning and herbivore exclusion) in three different habitat types to evaluate recruitment limitation for three rare and three common grassland species. I also examined pollinator visitation and identity on the study species (Kolb 2008, Ye et al. 2014).

## **Methods:**

### *Seedling Establishment Experiment*

#### *Study Site*

Research was performed at Beaver Meadow Audubon Center, a 324-acre wildlife refuge located in Java Township, Wyoming County, New York (NY) (42.6733°N 78.3846°W). The moderately hilly topography, ranging from 4756 m to 4920 m, was formed during glacial retreat, approximately 11,000 years ago (Vu Tien 1977). Soils on the refuge consist of gravelly loam, which is well drained, medium textured, alkaline outwash soil (Soil Conservation Service, 1956). The mixed hardwood forests consist of mostly second growth and mature forest. The open meadows were used primarily for potato and tree farming but are now managed as open habitat for wildlife (Vu Tien 1977).



### *Study Species*

Ontario blazingstar (*Liatris cylindracea*), sky-blue aster (*Symphyotrichum oolentangiensis*), and giant yellow hyssop (*Agastache nepetoides*) are three predominantly Midwestern prairie species that have persisted in WNY since glacial retreat (Eckle 2001, Norwacki & Abrams 2008). These species are all threatened or endangered in NY (Table 1). Boneset (*Eupatorium perfoliatum*), New England aster (*Symphyotrichum novae-angliae*), and purple giant hyssop (*Agastache scrophulariifolia*) are three common species that were chosen because they are close relatives of the three rare species and are common throughout their range. *Symphyotrichum novae-angliae* and *A. scrophulariifolia* were selected as closely related congeners of *S. oolentangiensis* and *A. nepetoides*, but all other *Liatris* genera native to New York State also are either threatened or endangered. Based on phylogeny, the genus *Eupatorium* is considered the closest *Liatris* relative in the study area (Schmidt & Schilling 2000) and so *E. perfoliatum* was used as the common comparison species for *L. cylindracea*. Each common species is secure in NY (Table 1).

With the exception of *A. nepetoides*, which prefers moist, rich, open woodland areas (Fernald 1950, Gleason 1952, Gleason & Cronquist 1991, Toomey & Toomey 2002), the five remaining species inhabit dry, open sites and prefer limey to acidic, sandy, loamy, or rocky soils in open woods, prairie remnants, dunes, and bluffs (Burns 1983, Corrigan 2002, Young 2010, New York Natural Heritage Program 2013). The three rare species are declining throughout the northeastern United States due to habitat loss, habitat modification, exotic species invasion, excessive mowing, and ecological succession (Toomey & Toomey 2002, Young 2010). Some populations of *L. cylindracea* experience low pollination rates and limited seed dispersal (Gaiser 1951, Schaal 1974).

### *Seedling Establishment Experimental Design*

Experimental seed additions were combined with microhabitat manipulation to test recruitment limitation in three different habitat types: mature forest, forest edge and open meadow. There were three distinct habitat types at Beaver Meadow: second-growth deciduous woodlands (forest), open, annually mowed fields (meadow) and forest-meadow ecotone dominated by invasive shrubs (edge). In the spring of 2014, six locations were randomly chosen and transects established that bisected the ecotones with meadow, edge and forest experimental grids 10 m apart. The experimental grids were 1.5 m<sup>2</sup> ( $n = 18$  total). Each grid contained four, 0.5 x 0.5 m treatment plots: burn (burned), deer (deer exclusion), burn + deer and control (no treatment) separated by 0.5 m (Fig. 1). For the burn treatment, I used a handheld propane torch to burn away all vegetation and standing litter immediately prior to the beginning of the growing season. The deer exclusion treatment consisted of a 0.5 x 0.5 x 0.5 m PVC frame (secured to the ground with two rebar) covered in bird netting (held to the frame by cable straps) to prevent browse on the study species (MacDougall & Wilson 2007). Treatment type and seed planting location within the grids were selected randomly.

Seeds of *A. nepetoides* were collected in the fall of 2013 at a Western New York Land Conservancy site in Lockport, NY (43.193125°N, -78.733749°W). Average seed weight for this species was 0.356 mg. Seeds of *E. perfoliatum* and *S. novae-angliae* were collected from meadows in Marilla, NY (42.817718°N, -78.501267°W). Seeds of *L. cylindracea*, *S. oolentangiensis* and *A. scrophulariifolia* were too rare or uncommon to collect in WNY, and they were purchased from Prairie Moon Nursery (Winona, MN). Average seed weights for these species were 0.12 mg (*E. perfoliatum*), 0.248 mg (*S. novae-angliae*), 2.32 mg (*L. cylindracea*), 0.232 mg (*S. oolentangiensis*), and 0.476 mg (*A. scrophulariifolia*). The seeds were cold

stratified at 2.5 °C for two months to break seed dormancy. Stratified seeds were placed in plastic bags with a tablespoon of potting soil to ensure soil to seed contact upon sowing. Each treatment plot contained 6 subplots (one for each species), which were separated by 0.5 m and each was planted with 10 seeds of the study species. Each plot was covered with a wood fiber seed blanket held down with landscape pins to protect the seeds and keep them from washing away during heavy rainfall.

All plots were checked twice a week for germination. Plot sampling order was haphazard to avoid bias of order. To ensure accuracy in identification, seedlings in the plots were visually compared to seedlings germinated in the lab. Soil moisture and temperature were measured weekly using a HydroSense II soil probe (Campbell Scientific, Inc., Logan, UT, USA) and a Taylor soil thermometer (Taylor Precision Products, Oak Brook, IL, USA). Photosynthetically active radiation (PAR; wavelength: 400-700 nm) was measured using a 0.5 m handheld AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA, USA), and reference PAR was measured using a LI-200 spherical PAR sensor (LiCor, Inc., Lincoln, NE, USA). Midday PAR measurements were taken in July after full tree canopy leaf out. Percent herbaceous cover for each plot was measured bimonthly by breaking the plots into a 10 x 10 grid and observing how many cells were covered with growing plant material. At the end of the growing season, above ground biomass was harvested for both the study species as well as all other plants growing in each plot. The plants were cut at the level of the soil, placed in a paper bag, and placed in a drying oven for 3 days at 65 °C. After 3 days, plant matter was removed and weighed.

### *Pollinator Observation*

### *Study Sites*

Pollinator observations took place at five different locations – Hunter’s Creek Park in Wales, New York (42.737°N, -78.5512°W), an open meadow in Marilla, New York (42.794322°N, -78.556849°W), Beaver Meadow Audubon Center in Java, New York (42.6733°N, -78.3846°W), and Whirlpool State Park (43.1170° N, -79.0610° W) and Devil’s Hole State Park in Niagara Falls, New York (43.1325°N, -79.047°W). With the exception of Devil’s Hole State Park, each site consisted of large expanses of open habitat dominated by grasses and forbs. Little to no shrub cover was present. Devil’s Hole is located within the Niagara River gorge and is bordered by sheer limestone cliffs to the west and the Niagara River to the east. Populations of the study species were located on exposed cliff faces wherever there were cracks large enough for soil development.

#### *Pollinator Observation Study Design*

Pollinator observations were made for each species during their blooming period – July for *L. cylindracea* and *Eupatorium perfoliatum* and August through September for *S. oolentangiensis* and *S.novae-angliae*. In areas where *E. perfoliatum* co-occurred with other *Eupatorium* spp., those were observed as well. Populations of *A. scrophulariifolia* are no longer found in western New York. A series of randomized 1m<sup>2</sup> plots were established in the wild populations of each species. Available flowers were tallied within the plot and observations consisted of filming the flowers in 5-minute segments for a total of 20 minutes worth of observations for each plot. This process was repeated for each plot for a minimum of 2 hours of observation on any given day. Observations were taken on fair weather days at a standardized time between 12:00 PM and 4:00 PM to eliminate any potential temporal bias. Observations were video recorded using a handheld digital camcorder (Samsung model HMX-F80) to record each 5-minute session (Ye et al. 2014).

The film was then analyzed for pollinator identity and visitation ratio. A visit was counted if the pollinator actively probed the flowers. Each flower visited by a single pollinator was counted only once towards the overall visitation ratio. Repeated flower visits by the same pollinator were not counted. For each observation, the type of pollinator that visited most frequently was coded as the dominant pollinator type for that session. Pollinator visits were then converted to a ratio of total flowers visited over the total flowers available.

### *Data Analysis*

Germination (germinated seeds/planted seeds) and survival (surviving seedlings/germinated seeds) were evaluated as binomial proportions using generalized linear models (GLMs) assuming binomial error distributions. Species and treatments were included as factors and evaluated using analysis of variance (ANOVA) using a Chi-square test instead of F-test (because the data are binomial). Model selection was based on Akaike information criterion (AIC). Overdispersion was  $< 1.15$  in both models. I evaluated species differences in a separate model than rarity because the two terms were collinear. Using Variance inflation factors (VIF) analyzed in the ‘car’ package for the R statistical programming environment (R Development Core Team, 2005), I found that none of the other terms were collinear ( $VIF < 2.5$ ). I used a GLM for germination differences and treatment effects. Because ecological field studies are challenged by a balance between false hits (Type I error) and missing true hits (Type II error), I considered coefficients with  $p$  values of  $< 0.05$  as significant and  $p$  values of  $< 0.10$  as marginally significant (*sensu* Hurlbert & Lonbardi 2009).

GLMs also were used to evaluate germination and survival as a function of continuous soil moisture, temperature, diffuse light and biomass as continuous variables and rarity as a

factor an analysis of covariance (ANCOVA) models. Model selection was based on Akaike information criterion (AIC). Overdispersion was  $<1.0$  in both models. None of the terms were collinear (VIF  $<1.10$ ). Continuous variables were scaled. The mixed models were fit using the Laplace approximation ‘lme4’ package (Bates & Maechler, 2009) for the R statistical programming environment (R Development Core Team, 2005).

I tested for biomass limits on germination at the 99<sup>th</sup>, 95<sup>th</sup>, and 90<sup>th</sup> quantiles using the “bootstrap” method of the “quantreg” package (Koenker 2008) for R for estimating the regression coefficients. Because of the complexity inherent in ecological systems, quantile regression can be used to assess a potential limiting factor that constrains all responses that may not have been directly measured (Cade and Noon 2003).

Pollinator visitations were examined using a *t*-test to compare mean between-species pollinator visitation rates for the rare species and their common congeners. I assessed differences in pollinator types using an ANOVA.

## **Results:**

### *Seedling establishment experiments*

Habitat types had similar soil moisture and temperature. There were considerable differences in the amount of PAR, with the forest habitat receiving the least amount. The differences in diffuse light were the result of the differences in vegetation type between each habitat (Table 2).

Germination success differed marginally significantly between study species ( $df = 5$ ,  $p$ -value = 0.073). Post-hoc results indicated that only *E. perfoliatum* (mean = 3.20%) and *S.novae-angliae* (mean = 5.33%) differed from the rest of the plants, as well as each other ( $p$  value = 0.042) [Fig. 2]. None of the study species had average germination rates  $> 5\%$ .

Germination was not affected by habitat type ( $df = 2$ ,  $p$  value = 0.126), but was influenced by transect ( $df = 5$ ,  $p$  value = < 0.001) as transect 1 had twice the germination (6.8%) as any other transect. A significant treatment X rarity interaction term ( $df = 3$ ,  $p$  value = 0.015) indicated that rare species was greater than common species germination in burn treatments (mean  $\pm$  SE, rare =  $6.30 \pm 1.46$ , common =  $3.90 \pm 0.85$ ) whereas common species was greater than rare species germination in exclosure treatments (rare =  $1.30 \pm 0.53$ , common =  $3.15 \pm 0.95$ ) [Fig. 3]. All species germination was greater in the burn and burn + exclosure treatments than the control plots [Fig. 3].

I only found an estimatable fitted line for the influence of biomass on rare plant germination at the 99<sup>th</sup> quantile ( $coeff.$  = -125,  $SE$  = 55.566,  $t$ -value = -2.237,  $p$  value = 0.026) [Fig. 4A]. Conversely this was not the case for common species ( $coeff.$  = 0,  $SE$  = 113.841,  $t$ -value = 0,  $p$  value = 1). Only rare species germination was limited by biomass density [Fig. 4B].

Survival did not differ significantly ( $df = 5$ ,  $p$  value = 0.147) between study species and was not greater than 15% overall [Fig. 5]. It also was not affected by transect ( $df = 5$ ,  $p$  value = 0.194), but did differ by treatment ( $df = 3$ ,  $p$  value = 0.017) as plants in the control had a mean survival  $0\% \pm 0$ , burn  $4.167\% \pm 3.069$ , exclusion  $2.941\% \pm 2.941$ , and burn + exclusion  $17.063\% \pm 5.637$ . A significant habitat X rarity interaction term ( $df = 2$ ,  $p$  value = 0.041) indicated that survival for all species was lowest in the edge habitats (no survival) and highest in the forest habitat (*L. cylindracea* =  $1.25\% \pm 1.25$ , *A. nepetoides* = 0%, *S. oolentangiensis* =  $0.83\% \pm 1.25$ , *E. perfoliatum* =  $0.42\% \pm 1.25$ , *A. scrophulariifolia* = 0%, *S. novae-angliae* = 0%), but common species survived much better in meadow habitat (*L. cylindracea* =  $0.83 \pm 0.58$ , *A. nepetoides* = 0%, *S. oolentangiensis* = 0%, *E. perfoliatum* = 0%, *A. scrophulariifolia* =  $0.83\% \pm 0.58$ , *S. novae-angliae* =  $0.83\% \pm 0.58$ ) than rare species (no survival) [Fig. 6].

### *Pollinator Observations*

Mean ( $\pm$  SE) flower visitation was significantly higher at *Eupatorium spp.* (mean =  $0.43 \text{ hour}^{-1} \pm 0.10$ ) than *L. cylindracea* (mean =  $0.21 \text{ hour}^{-1} \pm 0.08$ ) ( $t = -1.689$ ,  $df = 24.863$ ,  $p \text{ value} = 0.052$ ) [Fig. 7a], but pollinator visitation did not significantly differ ( $t = -0.203$ ,  $df = 35.996$ ,  $p \text{ value} = 0.420$ ) between *S. oolentangiensis* (mean =  $0.09 \text{ hour}^{-1} \pm 0.04$ ) and *S. novae-angliae* (mean =  $0.10 \text{ hour}^{-1} \pm 0.04$ ) [Fig. 7b]. Dominant pollinator taxon differed marginally significantly between all observed plant species ( $df = 6$ ,  $f\text{-value} = 2.28$ ,  $p \text{ value} = 0.061$ ). Long tongue bees in genus *Bombus* were the dominant pollinators visiting all four of the plant species sampled (visitation =  $18.5\% \pm 4.45$ ).

### **Discussion:**

Rare grassland species do not compete well with other plants. They successfully germinated where burning reduced initial competitor density, but otherwise appeared severely limited by interspecific competition. Once germinated, however, they did not survive in open meadow habitats as other plants recovered from the burn disturbance. Conversely, the common study species did well in these highly competitive conditions. Both rare and common grassland species germinated and survived the first growing season in forest habitats where shading limited competitors. Finally, pollinator limitation may explain grassland plant rarity for at least one of my study species, which suggests that diminished populations may not offer enough of a floral cue for pollinator search images.

Disturbance plays a considerable role in plant community assembly (White & Jentsch 2004). Burning increased germination considerably, especially for the rare grassland species, as



it does for grassland species worldwide (Collins & Barber 1986, Waldrop et al. 1992, Briggs et al. 2002, Brockway et al. 2002, Harrison et al. 2003, Briggs et al. 2005). Seedling establishment decreases with species richness in grassland habitats (Tilman 1997). Grassland species in northeastern N.A. may persist as tolerators rather than competitors (*sensu* Grime 1977). As such, they may do well in adverse habitat conditions that limit the establishment of highly competitive common plant species. Competitor density, as indicated by interspecific plant biomass, limited rare species recruitment in this study, but had no impact on the common species. Burning reduces interspecific competition (Juttila et al. 2002), suggesting that rare species are poor competitors for resources such as space, light, and nutrients (Grime 1977). As such, rare grassland species persistence in northeastern N.A. may be due to widespread burning by early humans (Steuter 1991, Nowacki & Abrams 2008).

Ecological responses to fire are dynamic (Brockway et al. 2002), however, and may increase non-native plant invasions or decrease native plant diversity depending on the extent and severity of the burn (Collins & Barber 1986, Keeley et al. 2003). Both the rare and common grassland species studied here germinated and survived poorly in the edge habitat, which was dominated by invasive shrub species such as multiflora rose (*Rosa multiflora*) and Japanese honeysuckle (*Lonicera* spp.). Generally, natural fire regimes inhibit woody encroachment (Van Auken 2009, Ratajczak et al. 2011), and potentially would increase suitable habitat for the grassland species, but the burning treatment employed here only impacted the herbaceous layer. Similarly, Standish et al. (2007) showed that native recruitment in abandoned fields was hampered by the presence of a few dominant non-native plant species. Whereas habitat type did not affect germination, survival was greatest for both common and rare species in the forest habitat. This pattern likely was due to reduced competition from understory herbaceous plants as

the forest plots had the lowest herbaceous vegetation cover. Given that the rare and common species survived equally well in the forest and edge habitats, but common species did much better in the meadows, the competition for space may be the limiting factor for rare species as interspecific vegetation recovered after burning much faster in this habitat than the others. Historically, grassland species in northeastern NA occupied nutrient and moisture poor habitats until increased nutrient loads allowed more competitive species as well as woody encroachment (Hamilton 2012). Despite the importance of recruitment in plant community assembly, long-term survival following germination also needs consideration. Whereas first-year survival was highest in the forest habitats, longer term study is needed to determine of the plants can persist – particularly as grassland species reproduction often is limited by shading (McKinney & Goodell 2010).

*Liatris cylindracea* received fewer pollinator visits per flower than *Eupatorium* spp. This discrepancy between the rare and common species may indicate that pollinator limitation also explains the difference in the relative abundances in these plant species in northeastern N.A. In contrast, there were no differences in pollinator visitation between *S. oolentangiensis* and *S. novae-angliae*. For plants, there are often minimum populations sizes required to attract pollinators (Klinkhamer et al. 1989, Klinkhamer & de Jong 1990, Robertson & Macnair 1995, Brys et al. 2008). Variations in estimated sampled population sizes between *Eupatorium* spp. and *L. cylindracea* may explain the discrepancies in pollinator visits between these two groups, however, this is in need of further investigation (Brys et al. 2008). Bumblebees (*Bombus* spp.) were the dominant pollinator type for all study species. Plant population size may explain the differences in visitation because bumblebees tend to favor flowers in high-density patches as a way of limiting flight distances while foraging (Klinkhamer & de Jong 1990). Although I

analyzed visitation ratios per flower, I cannot discount the effects of community context – conspecific and heterospecific flower diversity, and pollinator abundance – on the visitation ratios of my study species. Pollinator effectiveness also plays a role in plant reproduction (Larson 2005). Plants visited by a suite of generalist pollinators, which includes *Bombus* spp., receive less pollen than those visited by specialist pollinators (Larson 2005). Another avenue of investigation would be to examine the effects of pollinator type and visitation on reproductive output (i.e. seed production and viability) for the rare and common species. Finally, a comparison between effective pollinators in habitat where the rare species are common, e.g., midwestern U.S., and rare would indicate whether the rare species require specialized, co-evolved pollinators.

Commonness and rarity are temporal designations that can change as disturbance alters the landscape. The results of this experiment clearly demonstrate rarity as a function of habitat limitation and, to a lesser degree, dispersal limitation. These factors are not distinct categories, but rather create a gradient along which rare and common species sort out. With shifts in climate and land-use, ecological community composition changes to favor those species best adapted to altered conditions. Species that once thrived in post-glacial, and possibly early anthropogenic, N.A. now find themselves in a radically different landscape. The results presented here suggest that rare species tolerate poor habitats that hinder the establishment of more competitive species. Preserving these rare species in remnant landscapes may require human management to set back the clock to suitable habitat conditions. For rare grassland plants, widespread burning and planting appears to be required, both to create suitable habitat and encourage positive biotic interactions.

## References:

- Ackerman, J. D., A. Sabat, and J. K. Zimmerman. "Seedling Establishment in an Epiphytic Orchid: An Experimental Study of Seed Limitation." *Oecologia* 106.2 (1996): 192-98. Print.
- Bates D, Maechler M (2009) lme4: linear mixed-effects models using Eigen and syntax R package version 0.999375-32. Available at <http://CRAN.R-project.org/package=lme4> (accessed December 2010).
- Bevill, R. L., and S. M. Louda. "Comparisons of Related Rare and Common Species in the Study of Plant Rarity." *Conservation Biology* 13.3 (1999): 493-98. Print.
- Briggs, John M., Alan K. Knapp, and Brent L. Brock. "Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions." *The American Midland Naturalist* 147.2 (2002): 287-294.
- Briggs, John M., et al. "An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland." *BioScience* 55.3 (2005): 243-254.
- Brockway, Dale G., Richard G. Gatewood, and Randi B. Paris. "Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons." *Journal of Environmental Management* 65.2 (2002): 135-152.
- Brown, J.H. & Heske, E.J. (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science*, 250, 1705– 1707.
- Bruno, J. F. "Causes of landscape-scale rarity in cobble beach plant communities." *Ecology* 83.8 (2002): 2304-14. Print.

- Brys, Rein, Hans Jacquemyn, and Martin Hermy. "Pollination efficiency and reproductive patterns in relation to local plant density, population size, and floral display in the rewarding *Listera ovata* (Orchidaceae)." *Botanical Journal of the Linnean Society* 157.4 (2008): 713-721.
- Cade, B. S. and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Cain, S. A., M. Nelson, and W. McLean. "Andropogonetum Hempsteadii: a Long Island grassland vegetation type." *The American Midland Naturalist* 18 (1937): 324-50. Print.
- Chambers, Jeanne C., and James A. MacMahon. "A Day in the Life of a Seed: Movements and Fates of Seed and Their Implications for Natural and Managed Systems." *Annual Review of Ecology and Systematics* 25 (1994): 263-92. Print.
- Clark, C. J., et al. "Are Plant Populations Seed Limited? A Critique and Meta-Analysis of Seed Addition Experiments." *The American Naturalist* 170.1 (2007): 128-42. Print.
- Clark, J. S. "Testing disturbance theory with long-term data: Alternative life-history solutions to the distribution of events." *American Naturalist* 148.6 (1996): 976-96. Print.
- Clark, James S., Eric Macklin, and Leslie Wood. "Stages and Spatial Scales of Recruitment Limitation in Southern Appalachian Forests." *Ecological Monographs* 68.2 (1998): 213-35. Print.
- Collins, Scott L., and Susan C. Barber. "Effects of disturbance on diversity in mixed-grass prairie." *Vegetatio* 64.2-3 (1986): 87-94.
- Corrigan, Elizabeth. 2002. *Agastache scrophulariifolia* (Willd.) Kuntze (purple giant hyssop) New England Conservation Program Conservation and Research Plan for New England. New England Wild Flower Society, Framingham, Massachusetts, USA.

- Coulson, Sarah J., et al. "Colonization of Grassland by Sown Species: Dispersal versus Microsite Limitation in Responses to Management." *Journal of Applied Ecology* 38.1 (2001): 204-16. Print.
- Cramer VA, Hobbs RJ, Standish RJ (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology and Evolution*:104-112.
- Crawley, M. J., and S. L. Brown. "Seed Limitation and the Dynamics of Feral Oilseed Rape on the M25 Motorway." *Proceedings: Biological Sciences* 259.1354 (1995): 49-54. Print.
- Crawley, M.J. (2000) Seed predators and plant population dynamics. *Seeds: the Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 167–182. CABI Publishing, Oxford.
- Dupouey, J. L., et al. "Irreversible Impact of past Land Use on Forest Soils and Biodiversity." *Ecology* 83.11 (2002): 2978-84. Print.
- Eckle, Patricia M. "The vascular flora of the vicinity of the falls of Niagara" Buffalo Museum of Science, 11 Jan. 2001. Web. 4 Dec. 2013.  
<<http://web.archive.org/web/20100531040930/http://www.mobot.org/plantscience/resbot/flor/wny-niag/flora.htm>>.
- Edmeades DC (2003). The long-term effects of manures and fertilisers on soil productivity and quality: A review. *Nutrient Cycling in Agrosystems* 66:165-180.
- Edwards, G.R. & Crawley, M.J. (1999) Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia*, 118, 288 –296.
- Ehrlén, Johan, and Ove Eriksson. "Dispersal Limitation and Patch Occupancy in Forest Herbs." *Ecology* 81.6 (2000): 1667-74. Print.

- Eriksson, O., and J. Ehrlén. "Seed and Microsite Limitation of Recruitment in Plant Populations." *Oecologia* 91.3 (1992): 360-64. Print.
- Fenner, M. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd ed. N.p.: CABI, 2000. Print.
- Fernald, M. L. *Gray's Manual of Botany*. 8th ed. New York: American Book Company, 1950. Print.
- Gaiser, Lulu O. "Evidence for Intersectional Field Hybrids in *Liatris*." *Evolution* 5 (1951): 52-67. Print.
- Garrott, R.A., White, P.J., White, C.A.V., 1993. Overabundance: an issue for conservation biologists? *Conserv. Biol.* 7, 946–949.
- Gleason, H. A. *The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada*. 3 vols. New York: New York Botanical Gardens, 1952. Print.
- Gleason, H. A., and A. Cronquist. *Manual of vascular plants of northeastern United States and adjacent Canada*. New York: New York Botanical Garden, 1991. Print.
- Gordon, R.B. 1939. The primeval forest types of southwestern New York. *New York State Museum Bulletin* 321: 1-102.
- Hamilton, K.G. Andrew. "Unraveling the Enigma of an Atlantic Prairie." *Northeastern Naturalist* 19.6 (2012): 13-42. Print.
- Harrison, S., B. D. Inouye, and H. D. Safford. "Ecological heterogeneity in the effects of grazing and fire on grassland diversity." *Conservation Biology* 17.3 (2003): 837-845.
- Hennig, Ernest Ireneusz, and Jaboury Ghazoul. "Plant–pollinator interactions within the urban environment." *Perspectives in Plant Ecology, Evolution and Systematics* 13.2 (2011): 137-150.

- Hobbie, Sarah E., and F. Stuart Chapin III. "The Response of Tundra Plant Biomass, Aboveground Production, Nitrogen, and CO<sub>2</sub> Flux to Experimental Warming." *Ecology* 79.5 (1998): 1526-44. Print.
- Howe, H.F. & Brown, J.S. (2000) Early consequences of rodent granivory on synthetic dicot communities. *Ecological Applications*, 10, 917–924.
- Howe, H.F. & Brown, J.S. (2001) The ghost of granivory past. *Ecology Letters*, 4, 371–378.
- Hubbell, S. P., et al. "Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest." *Science* 283.5401 (1999): 554-57. Print.
- Hurlbert SH, Lombardi CM (2009) Final collapse of the newmanpearson decision theoretic framework and the rise of the neofisherian. *Ann Zool Fennici* 46:311–49
- Juenger, Thomas, and Joy Bergelson. "Factors Limiting Rosette Recruitment in Scarlet Gilia, *Ipomopsis aggregata*: Seed and Disturbance Limitation." *Oecologia* 123.3 (2000): 358-63. Print.
- Jutila, Heli M., and James B. Grace. "Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis." *Journal of ecology* 90.2 (2002): 291-302.
- Keeley, Jon E., Daniel Lubin, and C. J. Fotheringham. "Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada." *Ecological applications* 13.5 (2003): 1355-1374.
- Klinkhamer, Peter GL, Tom J. de Jong, and Gerrit-Jan de Bruyn. "Plant size and pollinator visitation in *Cynoglossum officinale*." *Oikos* (1989): 201-204.
- Klinkhamer PGL, de Jong TJ. 1990. Effects of plant size, plant density and sex differential



- nectar reward on pollinator visitation in the protandrous *Echium vulgare* (Boraginaceae).  
*Oikos* 57: 399–403
- Koenker, R. 2008. Censored quantile regression redux. *Journal of Statistical Software* 27:1–24.
- Koerner, W., et al. " $\delta^{15}\text{N}$  of Forest Soil and Understorey Vegetation Reflect the Former  
Agricultural Land Use." *Oecologia* 21.3 (1999): 421-25. Print.
- Kolb, Annette. "Habitat fragmentation reduces plant fitness by disturbing pollination and  
modifying response to herbivory." *Biological Conservation* 141.10 (2008): 2540-2549.
- Lauenroth, William K. "Grassland primary production: North American grasslands in  
perspective." *Perspectives in grassland ecology*. Springer New York, 1979. 3-24. Print.
- Lázaro, Amparo, Anna Jakobsson, and Ørjan Totland. "How do pollinator visitation rate and  
seed set relate to species' floral traits and community context?" *Oecologia* 173.3 (2013):  
881-893.
- MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. *Ecology* 42: 594-598.
- MacDougall, Andrew S., and Scott D. Wilson. "Herbivory Limits Recruitment in an Old-Field  
Seed Addition Experiment." *Ecology* 88.5 (2007): 1105-11. Print.
- McGill, Brian J., et al. "Species abundance distributions: moving beyond single prediction  
theories to integration within an ecological framework." *Ecology Letters* 10 (2007): 995-  
1015. Print.
- McKinney, Amy M., and Karen Goodell. "Shading by invasive shrub reduces seed  
production and pollinator services in a native herb." *Biological Invasions* 12.8  
(2010): 2751-2763.

- Morris LR, Moraco TA, Leger E, Blank R, Sheley R (2013). Cultivation legacies alter soil nutrients and differentially affect plant species performance nearly a century after abandonment. *Plant Ecology* 214:831-844.
- Mosquin, Theodore. "Competition for pollinators as a stimulus for the evolution of flowering time." *Oikos* (1971): 398-402.
- Nathan, Ran, and Hellene C. Muller-Landau. "Spatial patterns of seed dispersal, their determinants and consequences for recruitment." *Trends in Ecology & Evolution* 15.7 (2000): 278-85. Print.
- New York Natural Heritage Program*. NYS DEC, 2014. Web. 17 Jan. 2014.  
<<http://www.dec.ny.gov/animals/29338.html>>.
- Nowacki, Gregory J., and Marc D. Abrams. "The Demise of Fire and "Mesophication" of Forests in the Eastern United States." *BioScience* 58.2 (2008): 123-38. Print.
- Overpeck, Jonathan T., Robert S. Webb, and Thompson Webb III. "Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future." *Geology* 20 (1992): 1071-74. Print.
- Peterson AT, Soberon J, Pearson RG, et al. 2011. Ecological niches and geographic distributions. Ecological niches and geographic distributions. Princeton, NJ USA: Princeton University Press.
- Pielou, E. C. *After the Ice Age : The Return of Life to Glaciated North America*. Chicago: University of Chicago Press, 1991. Print.
- Piqueray, Julien, Layla Saad, and Grégory Mahy. "Why some species cannot colonise restored habitats? The effects of seed and microsite availability." *Journal for Nature Conservation* 21 (2013): 189-97. Print.

- Preston, F. W. "The Commonness, and Rarity, of Species." *Ecology* 29.3 (1948): 254-83. Print.
- Primack, Richard B., and S. L. Miao. "Dispersal Can Limit Local Plant Distribution." *Conservation Biology* 6.4 (1992): 513-19. Print.
- Pulliam, H. Ronald. "On the relationship between niche and distribution." *Ecology letters* 3.4 (2000): 349-361. Print.
- R Development Core Team. (2005) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramankutty, Navin, and Jonathan A. Foley. "Estimating historical changes in global land cover: Croplands from 1700 to 1992." *Global Biogeochemical Cycles* 13.4 (1999): 997-1027. Print.
- Ratajczak, Zak, et al. "Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie." *Ecosphere* 2.11 (2011): art121.
- Robertson AW, Macnair MR. 1995. The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. *Oikos* 72: 106–114.
- Rooney, Thomas P., and Donald M. Waller. "Direct and indirect effects of white-tailed deer in forest ecosystems." *Forest Ecology and Management* 181.1 (2003): 165-176.
- Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *Am. Nat.* 137: S5-S28
- Schaal, Barbara A. "Isolation by Distance in *Liatris cylindracea*." *Nature* 252 (1974): 703. Print.

- Schmidt, Gregory J., and Edward E. Schilling. "Phylogeny and Biogeography of Eupatorium (Asteraceae: Eupatorieae) Based on Nuclear ITS Sequence Data." *American Journal of Botany* 87.5 (2000): 716-26. Print.
- Sih, Andrew, and Marie-Sylvie Baltus. "Patch size, pollinator behavior, and pollinator limitation in catnip." *Ecology* (1987): 1679-1690.
- Soil Conservation Service. 1956. Guide for Preparation of the Farm Conservation Plan (Buffalo Audubon Society). No. 930.
- Standish, R. J., et al. "Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia." *Journal of Applied Ecology* 44.2 (2007): 435-445.
- Steuter, Alan A. "Human Impacts on Biodiversity in America: Thoughts from the Grassland Biome." *Conservation Biology* 5.2 (1991): 136-37. Print.
- Stromayer, Karl AK, and Robert J. Warren. "Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities?." *Wildlife Society Bulletin* (1997): 227-234.
- Tilman, David. "Community Invasibility, Recruitment Limitation, and Grassland Biodiversity." *Ecology* 78.1 (1987): 81-92. Print.
- Toomey, B. and B. H Toomey. 2002. *Agastache nepetoides* (L.) Kuntze (Yellow Giant Hyssop) New England Plant Conservation Program Conservation and Research Plan for New England. New England Wild Flower Society, Framingham, Massachusetts, USA. <<http://www.newfs.org>>.
- Turnbull, Lindsay A., Michael J. Crawley, and Mark Rees. "Are Plant Populations Seed-Limited? A Review of Seed Sowing Experiments." *Oikos* 88.2 (2000): 225-38. Print.

- Van Auken, O. W. "Causes and consequences of woody plant encroachment into western North American grasslands." *Journal of Environmental Management* 90.10 (2009): 2931-2942.
- Van der Meijden, E., et al. "Meta-population dynamics of biennial plants - how to exploit temporary habitats." *Acta botanica neerlandica* 41 (1992): 249-70. Print.
- Verheyen, Kris, and Martin Hermy. "Recruitment and Growth of Herb-Layer Species with Different Colonizing Capacities in Ancient and Recent Forests." *Journal of Vegetation Science* 15.1 (2004): 125-34. Print.
- Vu Tien, Phuong-Chi. "A Vegetational Analysis of Selected Sites at Beaver Meadow Wildlife Refuge, Wyoming Count, New York." *Buffalo State College* (1977): 1-82. Print.
- Warren, Robert J., and Mark A. Bradford. "The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat." *Proceedings of the Royal Society B* 278 (2011): 1390-98. Print.
- Waldrop, Thomas A., David L. White, and Steven M. Jones. "Fire regimes for pine-grassland communities in the southeastern United States." *Forest Ecology and Management* 47.1 (1992): 195-210.
- White, PETER S., and A. N. K. E. Jentsch. "Disturbance, succession, and community assembly in terrestrial plant communities." *Assembly rules and restoration ecology: bridging the gap between theory and practice* (2004): 342-366.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251
- Ye, Zohng-Ming, et al. "Competition and facilitation among plants for pollination: can pollinator abundance shift the plant-plant interactions?" *Plant Ecology* 215 (2014): 3-13. Print.
- York, Julia (2012) "The Search for a Relict Prairie Graminoid Community in Western New York," *The Spectrum: A Scholars Day Journal: Vol. 2: Iss. 1, Article 12.*

Young, Stephen M., ed. "New York Natural Heritage Program Rare Plant Status Lists." *New York Natural Heritage Program*. NYS DEC, June 2010. Web. 6 Jan. 2014.

<[http://www.dec.ny.gov/docs/fish\\_marine\\_pdf/2010rareplantstatus.pdf](http://www.dec.ny.gov/docs/fish_marine_pdf/2010rareplantstatus.pdf)>.

Zeiter, M., et al. "Recruitment Limitation Constrains Local Species Richness and Productivity in Dry Grasslands." *Ecology* 87.4 (2006): 942-951. Print.

Table 1. State ranking system for plant species status in New York State demonstrating the ranking of experimental species (*New York Natural Heritage Program 2013*).

Table 1.

<b>Species</b>	<b>State Rank</b>	<b>Description</b>
<i>Liatrix cylindracea</i> , <i>Symphyotrichum</i> <i>oolentangiense</i>	S1	Critically imperiled in New York State because of extreme rarity (5 or fewer sites or very few remaining individuals) or extremely vulnerable to extirpation from New York State due to biological or human factors.
<i>Agastache nepetoides</i>	S2	Imperiled in New York State because of rarity (6 - 20 sites or few remaining individuals) or highly vulnerable to extirpation from New York State due to biological or human factors.
<i>Agastache nepetoides</i>	S3	Rare in New York State (usually 21 - 35 extant sites).
<i>Agastache scrophulariifolia</i>	S4	Apparently secure in New York State.
<i>Eupatorium perfoliatum</i> , <i>Symphyotrichum novae-</i> <i>angliae</i>	S5	Demonstrably secure in New York State.



Table 2. Average environmental parameters calculated for each habitat type during the summer of 2014

Table 2.

	<b>Meadow</b>	<b>Edge</b>	<b>Forest</b>
<b>Soil Moisture (%)</b>	27.08 + 0.41	25.57 + 0.36	24.32 + 0.32
<b>Soil Temp. (°C)</b>	18.80 + 0.06	17.48 + 0.02	17.40 + 0.04
<b>PAR (%)</b>	46.76 + 1.77	4.48 + 0.62	3.22 + 0.12

Figure 1 – Treatment grid design for experimental burning (burn) and herbivore exclusion (exclusion).

Figure 1

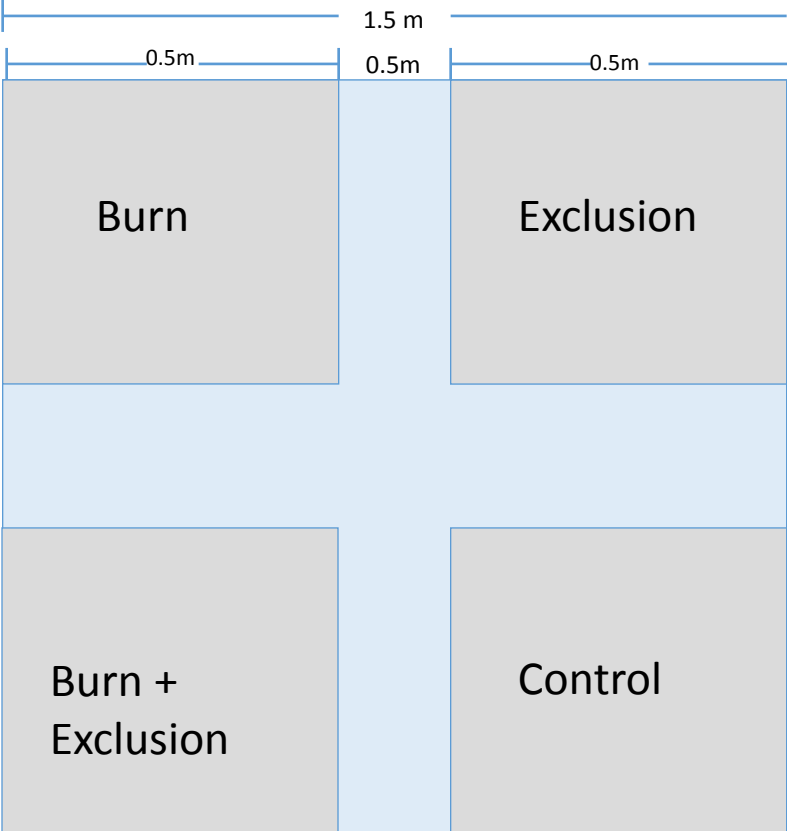


Figure 2. Mean ( $\pm$  SE) % germination for rare (white) and common (gray) grassland species. Means with different letters are significantly different.

Figure 2.

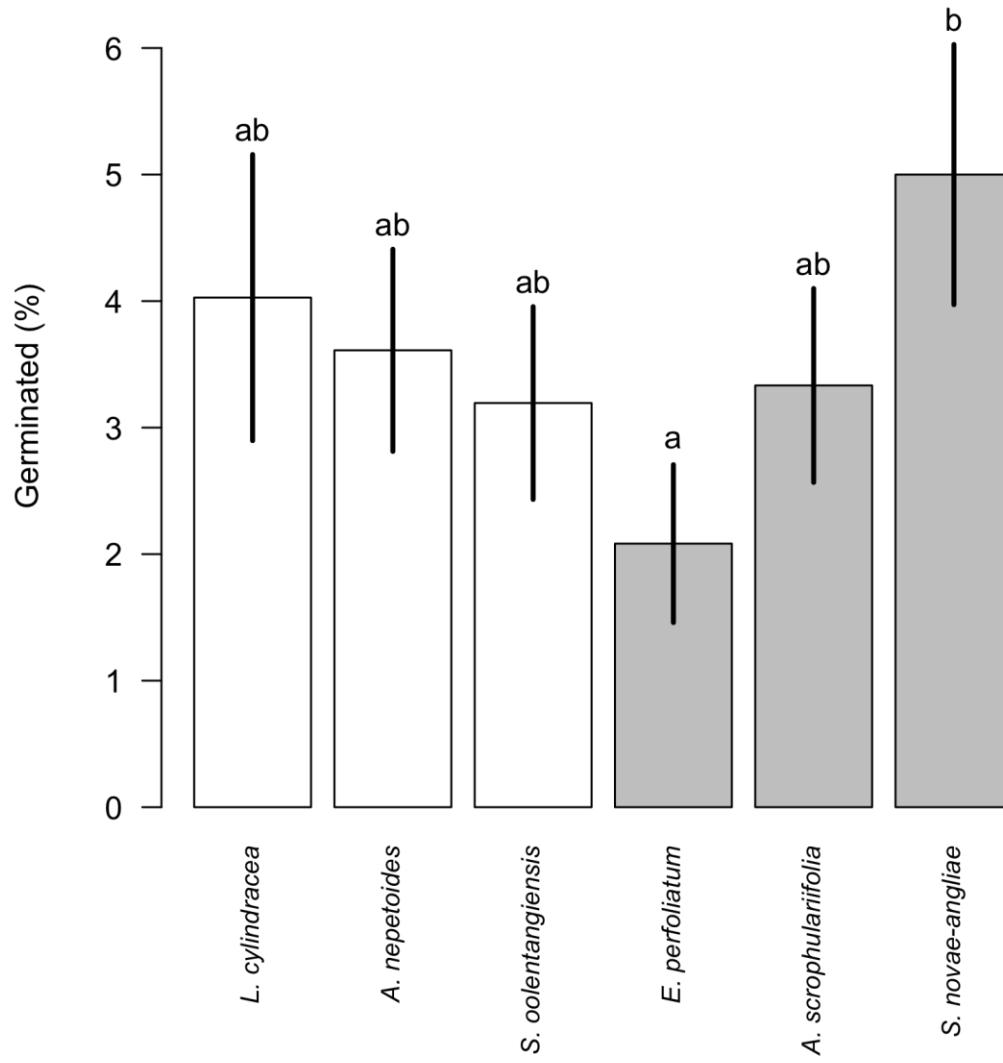


Figure 3. Treatment interaction plot showing mean ( $\pm$ SE) % germination across experimental treatments. Rare species germination was significantly higher than common species in the burn treatments whereas common species germination was significantly higher than rare in the exclosure treatments. Both rare and common species germination was higher in treatments that included burning.

Figure 3.

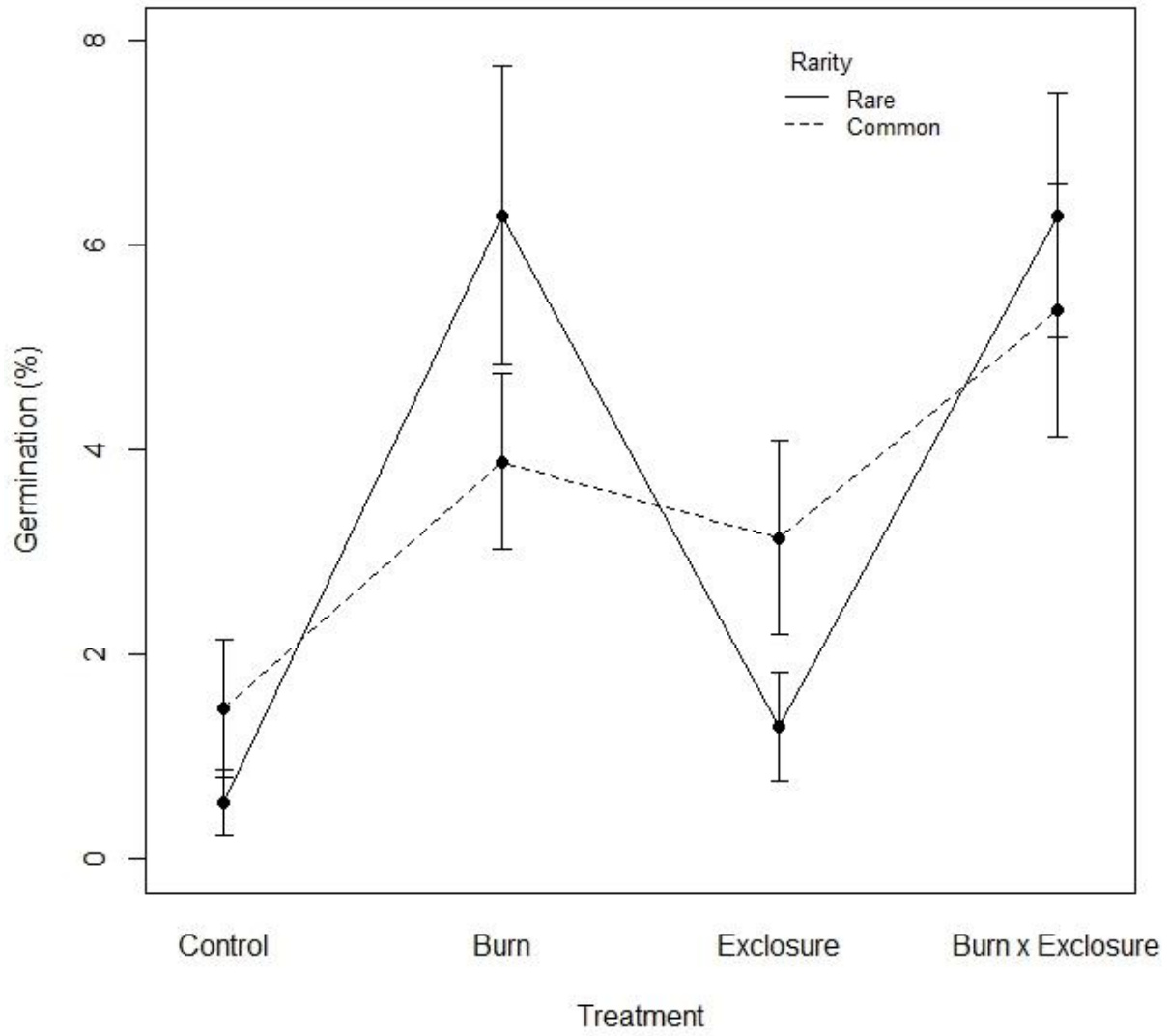




Figure 4. Quantile regression indicating that interspecific biomass set the upper limits on rare species germination (A) but not common species germination (B) at the 99<sup>th</sup> quantile.

Figure 4

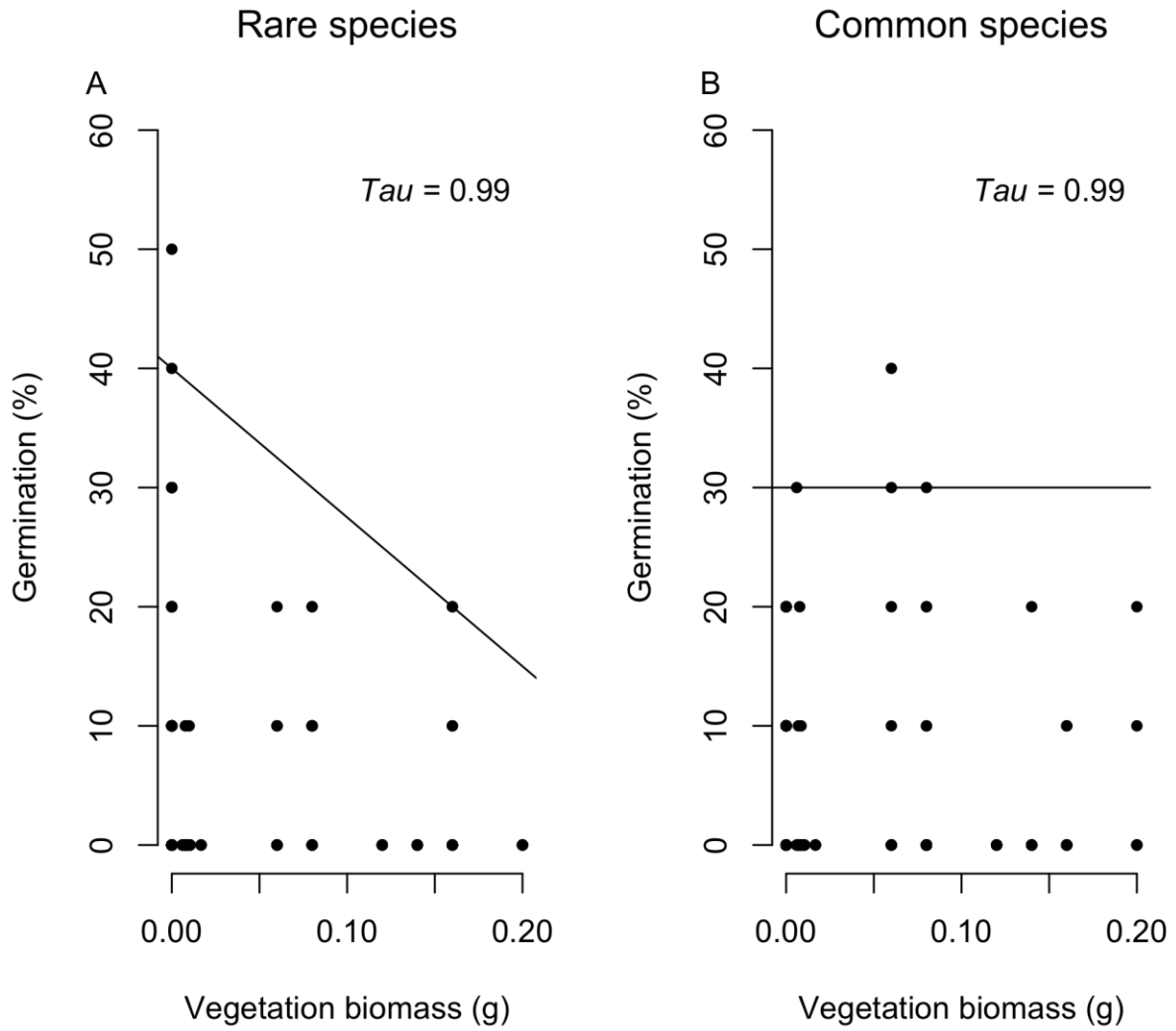


Figure 5. Mean ( $\pm$ SE) % survival for rare (white) and common (gray) species. There was no statistically significant difference in species survival, but none of the *Agastache nepetoides* plants survived

Figure 5

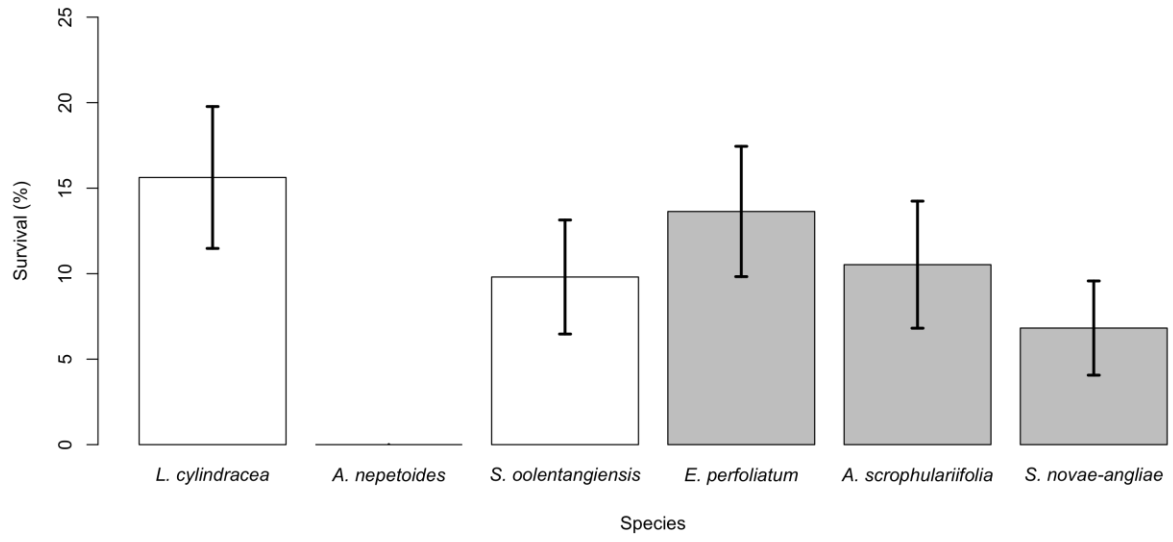


Figure 6. Habitat interaction plot showing mean ( $\pm$ SE) % survival. Both rare and common species survived equally poorly in edge habitat and equally better in forest habitat, but the common species survived significantly better in the meadow habitat than the rare species.

Figure 6

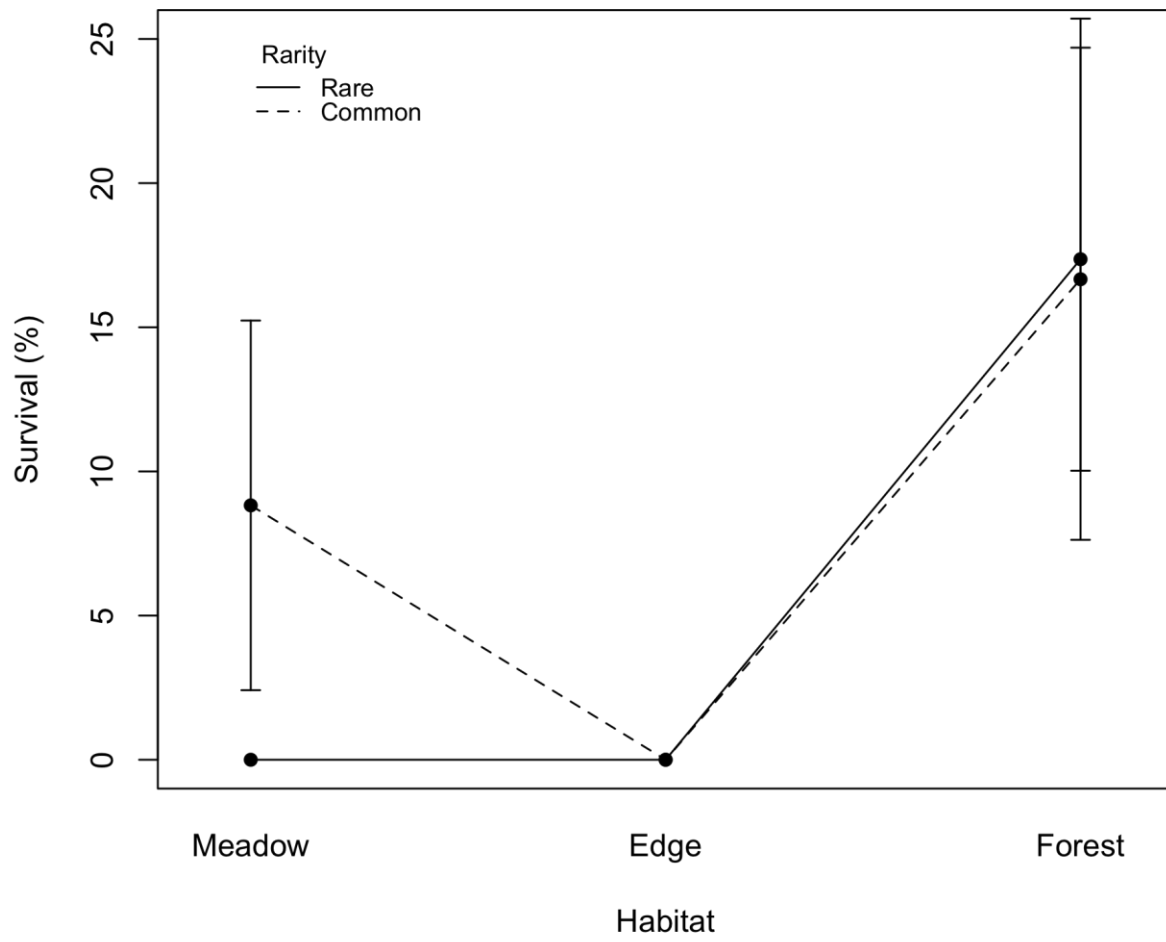


Figure 7. Mean ( $\pm$ SE) pollinator visitation per flower for rare (white) and common (gray) grassland species. Visitation was significantly greater for *Eupatorium perfoliatum* than *Liatris cylindracea* (a) but did not differ between *Symphiotrichum oolentangiensis* and *Symphiotrichum novae-angliae* (b).

Figure 7

