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Rareness Starts Early for Disturbance-Dependent Grassland Plant Species

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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

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Buffalo State College
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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. Commoness 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.

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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 virginian*) 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 at 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 at 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-angeliae* 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^2 (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 ^{o} 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 fore 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 ^{o}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^2 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 at 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 99th, 95th, and 90th 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 ± SE, rare = 6.30 ± 1.46, common = 3.90 ± 0.85) whereas common species was greater than rare species germination in exclosure treatments (rare = 1.30 ± 0.53, common = 3.15 ± 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 99th 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% ± 0, burn 4.167% ± 3.069, exclusion 2.941% ± 2.941, and burn + exclusion 17.063% ± 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% ± 1.25, *A. nepetoides* = 0%, *S. oolentangiensis* = 0.83% ± 1.25, *E. perfoliatum* = 0.42% ± 1.25, *A. scrophulariifolia* 0%, *S.novae-angliae* = 0%), but common species survived much better in meadow habitat (*L. cylindracea* = 0.83 ± 0.58, *A. nepetoides* = 0%, *S. oolentangiensis* = 0%, *E. perfoliatum* = 0%, *A. scrophulariifolia* 0.83% ± 0.58, *S.novae-angliae* = 0.83% ± 0.58) than rare species (no survival) [Fig. 6].

Pollinator Observations

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

Commoness 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.

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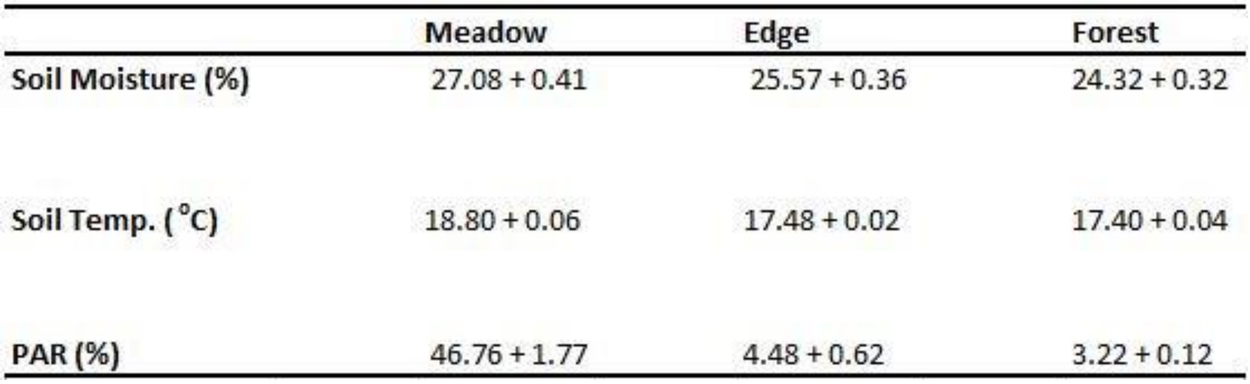
Table 1. State ranking system for plant species status in New York State demonstrating the ranking of experimental species (*New York Natural Heritage Program* 2013).

Table 1.

Species	**State Rank**	**Description**
Liatris cylindracea, Symphyotrichum oolentangiense	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.
Agastache nepetoides	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.
Agastache nepetoides	S3	Rare in New York State (usually 21 - 35 extant sites).
Agastache scrophulariifolia	S4	Apparently secure in New York State.
Eupatorium perfoliatum, Symphyotrichum novae-angliae	S5	Demonstrably secure in New York State.

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

Table 2.



	Meadow	Edge	Forest
Soil Moisture (%)	27.08 + 0.41	25.57 + 0.36	24.32 + 0.32
Soil Temp. (°C)	18.80 + 0.06	17.48 + 0.02	17.40 + 0.04
PAR (%)	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

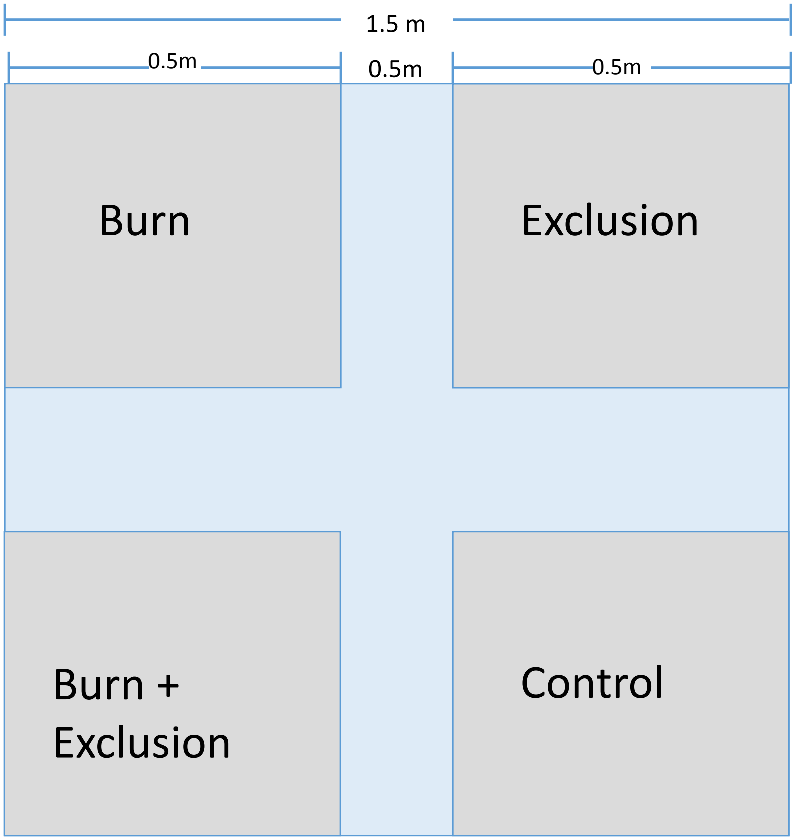


Figure 2. Mean (± SE) % germination for rare (white) and common (gray) grassland species. Means with different letters are significantly different.

Figure 2.

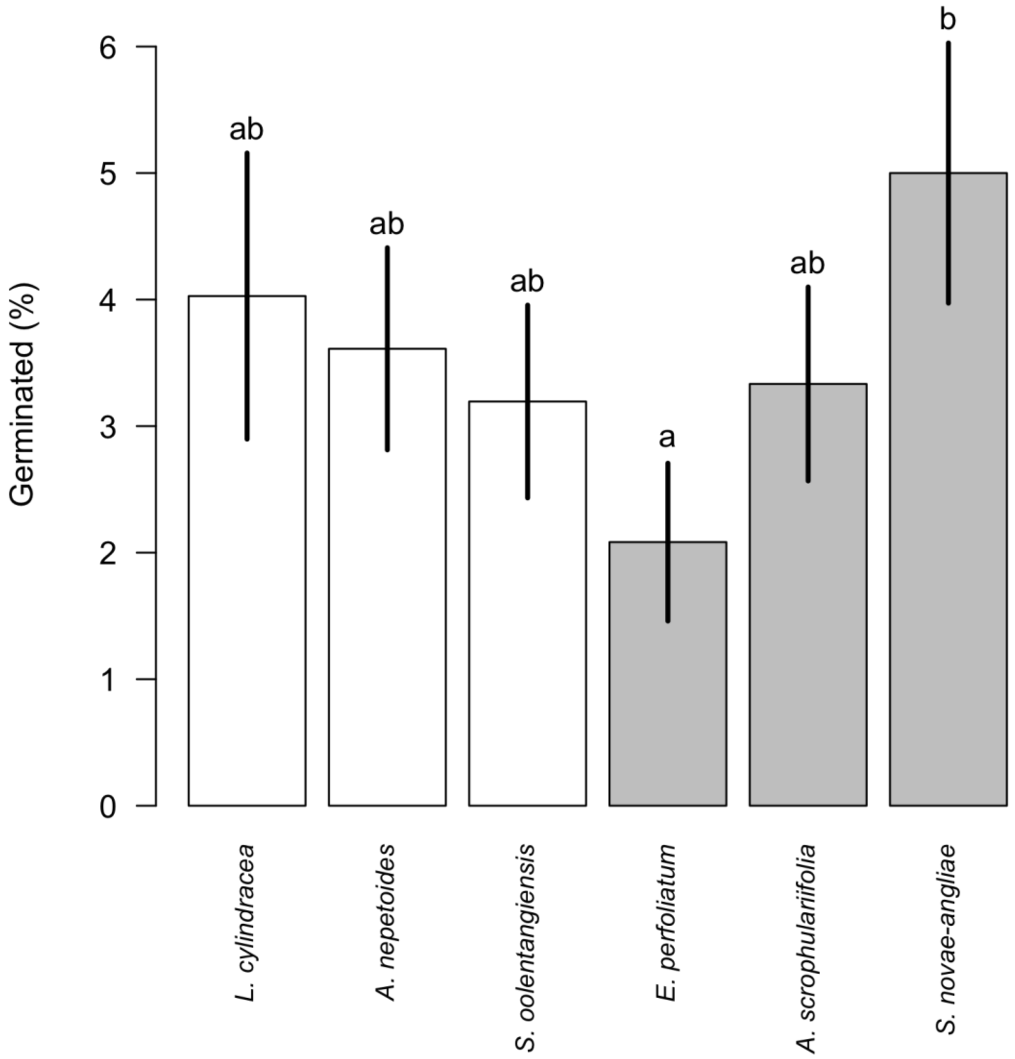

Germinated (%)
0
1
2
3
4
5
6
ab
ab
ab
a
ab
b
L. cylindracea
A. nepetoides
S. oolentangiensis
E. perfoliatum
A. scrophulariifolia
S. novae-angliae

Figure 3. Treatment interaction plot showing mean (±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.

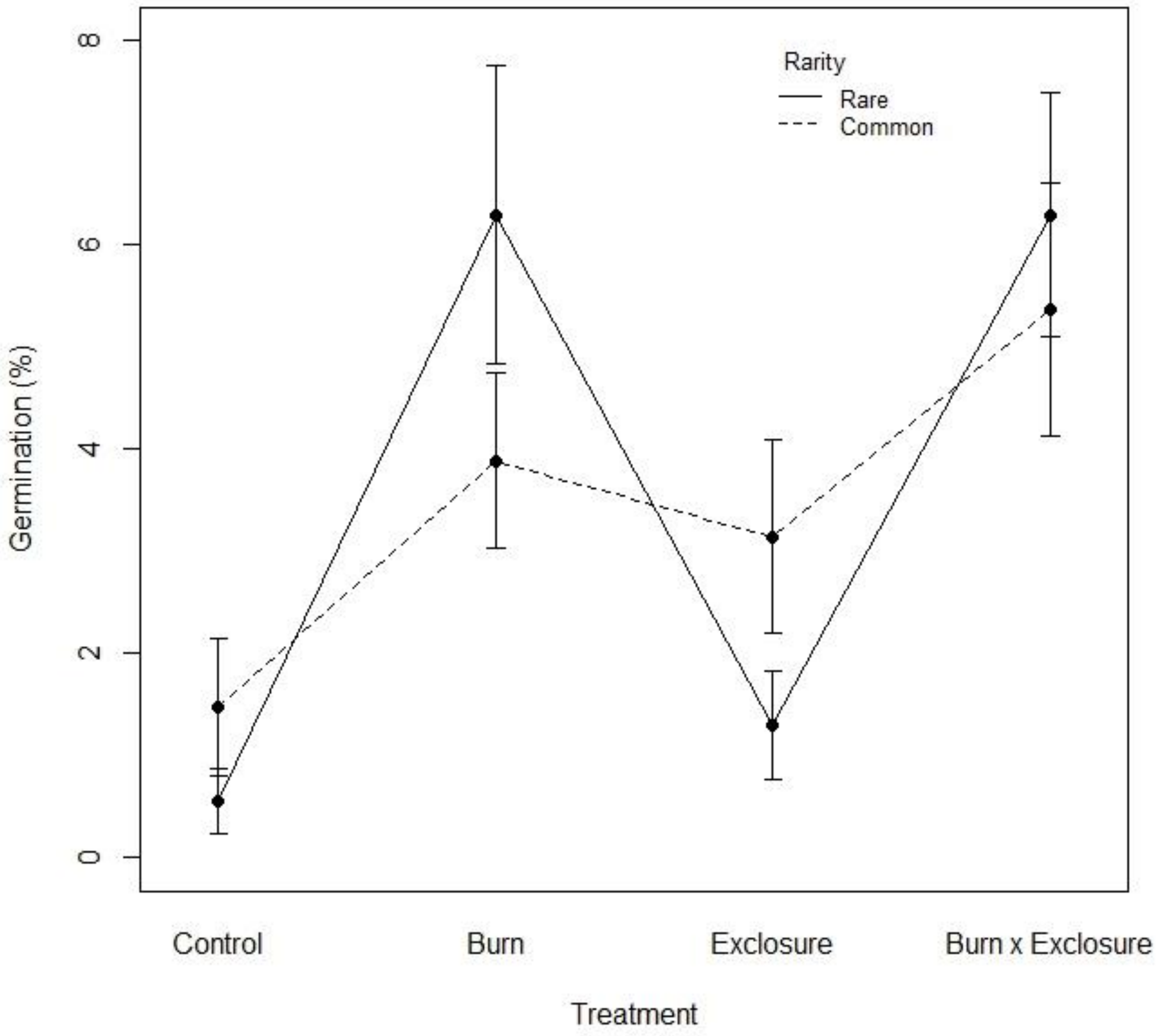

Rarity
Rare
Common
Germination (%)
0
2
4
6
8
Control
Burn
Exclosure
Burn x Exclosure
Treatment

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 99th quantile.

Figure 4

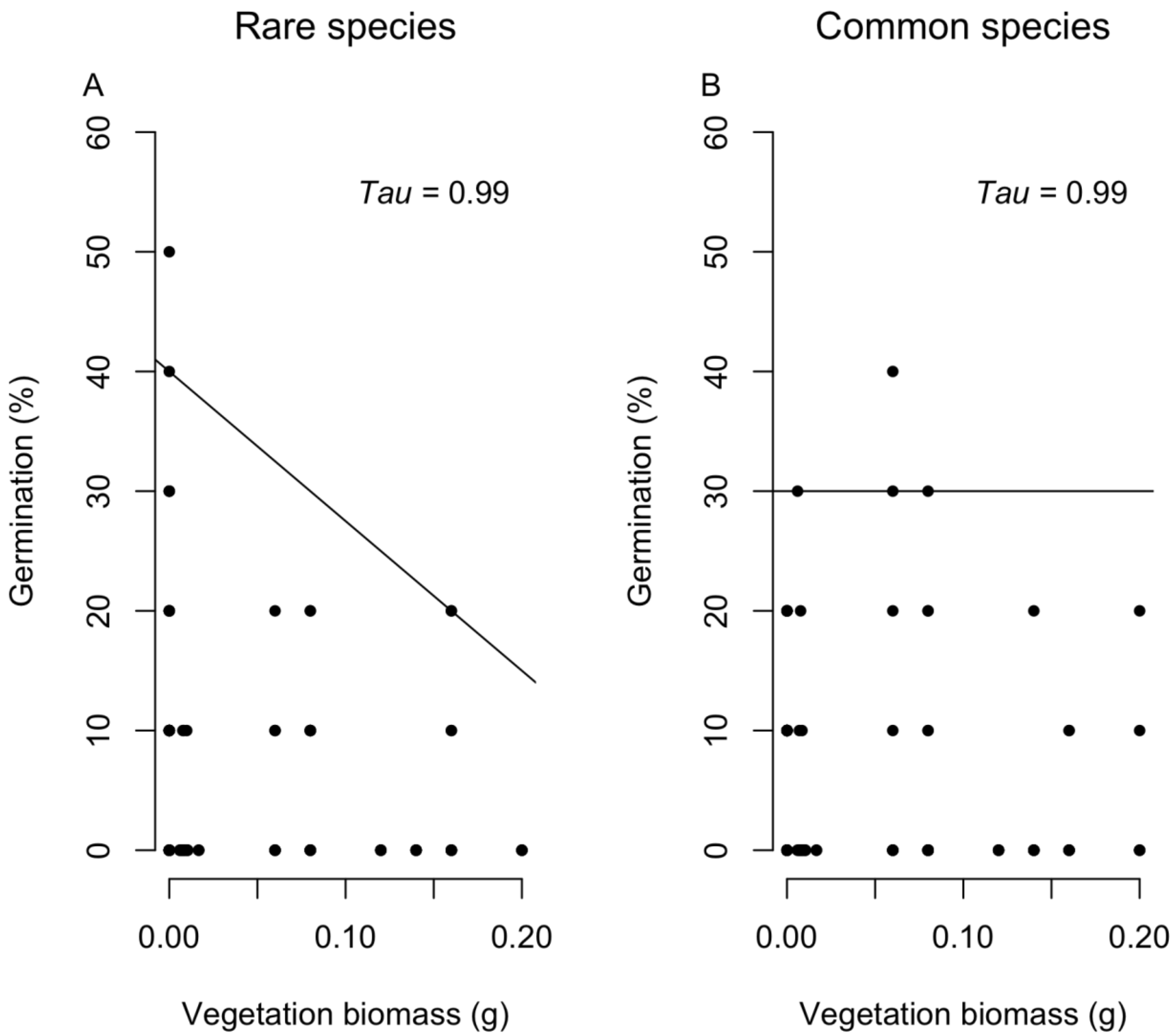
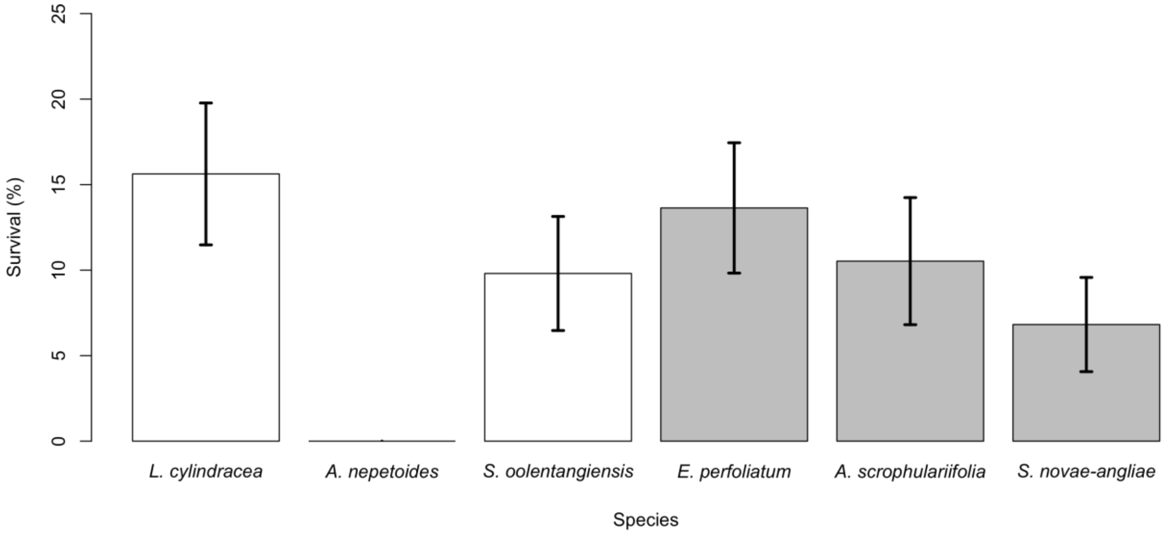

Rare species
Common species
A
B
Tau = 0.99
Tau = 0.99
Germination (%)
Germination (%)
0
10
20
30
40
50
60
0.00
0.10
0.20
Vegetation biomass (g)
Vegetation biomass (g)

Figure 5. Mean (±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

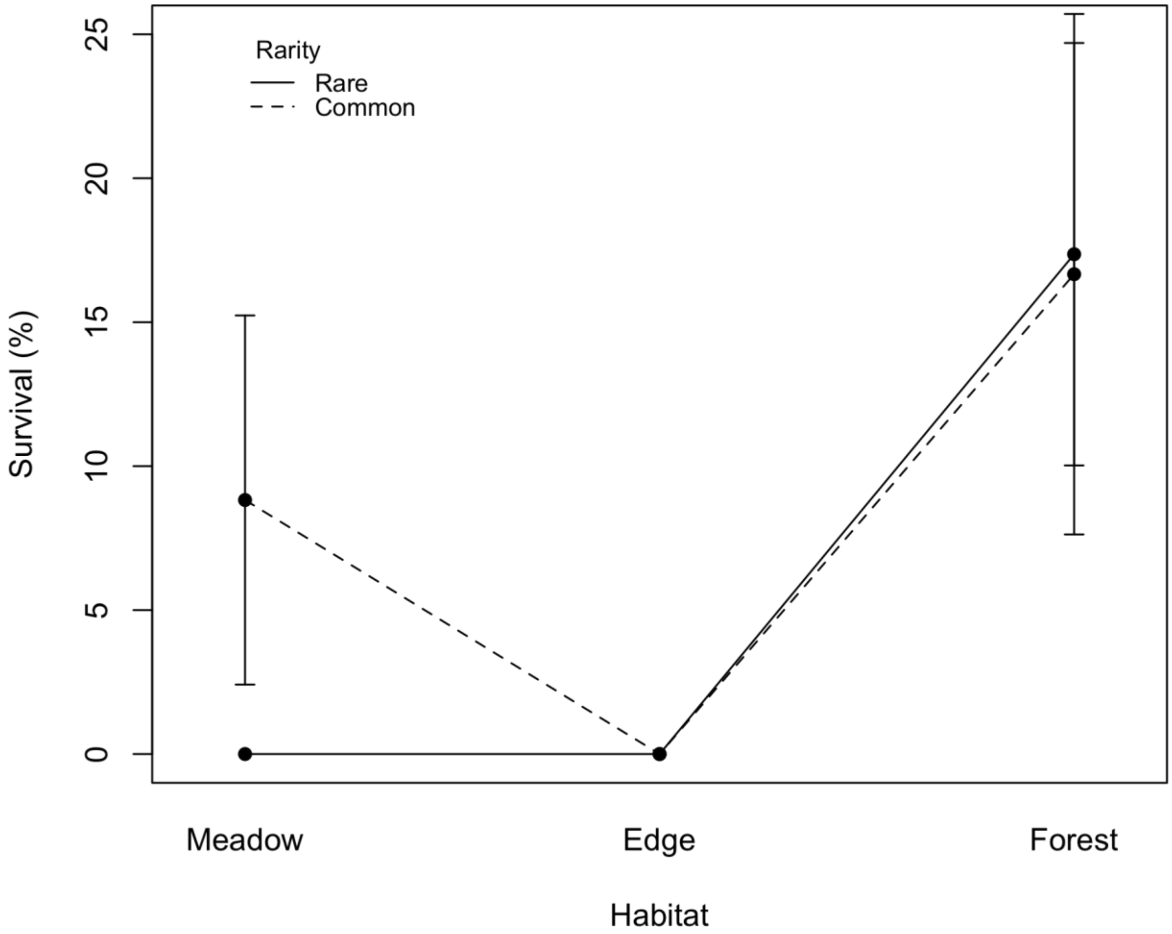
Figure 5



Survival (%)
0
5
10
15
20
25
L. cylindracea
A. nepetoides
S. oolentangiensis
E. perfoliatum
A. scrophulariifolia
S. novae-angliae
Species

Figure 6. Habitat interaction plot showing mean (±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.

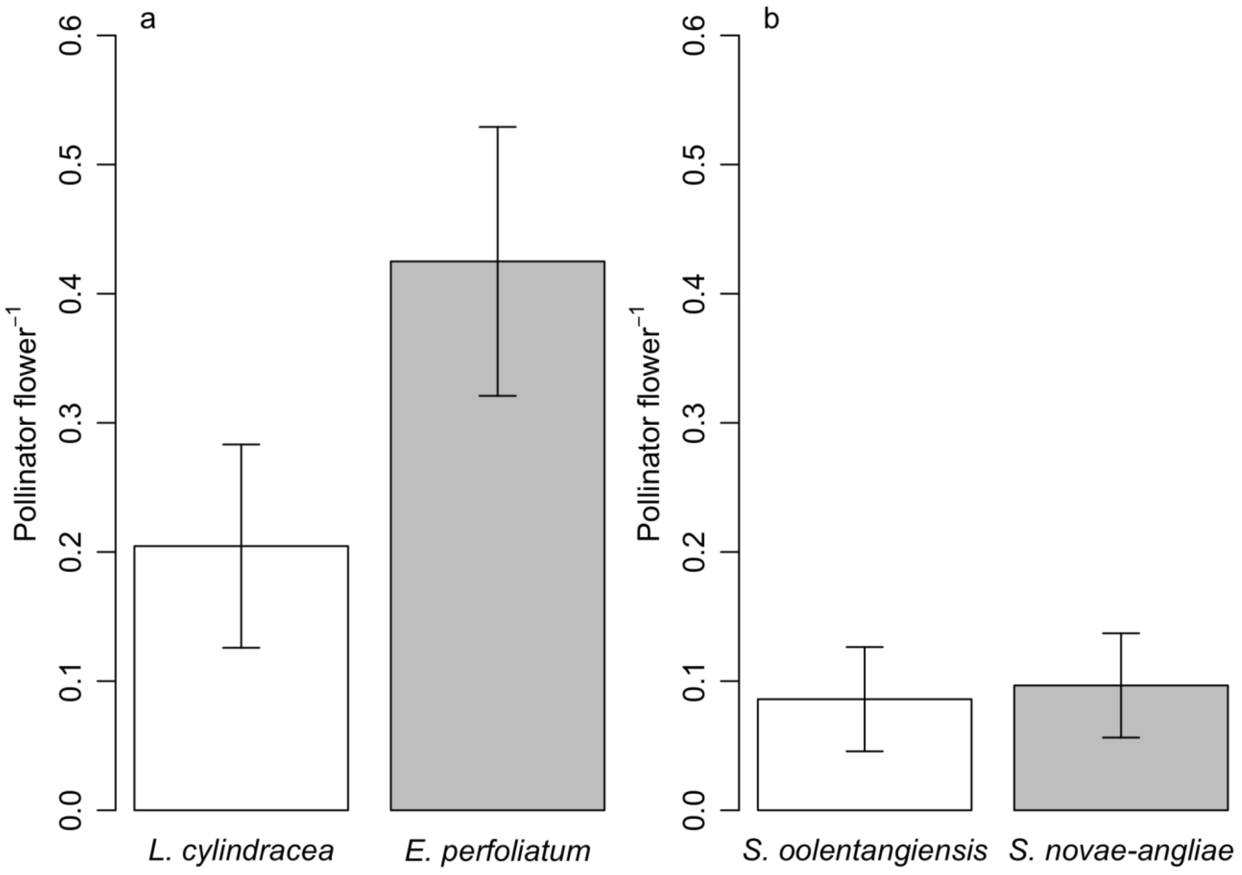
Figure 6



Rarity
Rare
Common
Survival (%)
0
5
10
15
20
25
Meadow
Edge
Forest
Habitat

Figure 7. Mean (±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


a
b
Pollinator flower^{-1}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
L. cylindracea
E. perfoliatum
S. oolentangiensis
S. novae-angliae