

Rareness starts early for disturbance-dependent grassland plant species

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Abstract Ecological communities always contain a few common species and an abundance of uncommon species. Given that most plant mortality occurs in seeds and seedlings, recruitment success often predicts plant community assemblage and patterning, but observational patterns do not reveal whether plant populations are seed or habitat limited. Grassland plant species make up a sizable portion of the overall native flora in northeastern North America (N.A.), but approximately 30 % of the area's threatened and endangered flora are grassland species, possibly leftovers from the post-glacial landscape. Yet, close relatives of many rare grassland species thrive in the same range. We investigated whether seed or habitat limitation explained rarity and commonness in remnant grassland species. We used seed addition experiments coupled with microhabitat manipulations (burning and herbivore exclusion) in three different habitat types to evaluate recruitment (germination and seedling survival) limitation for three rare and three common grassland species. Rare grassland species successfully recruited where burning reduced initial competitor density, but seedling survival suggested they were severely limited by interspecific competition. Both the rare and common plant species survived equally well in forest habitats where herbaceous density was low whereas neither survived in the edge habitats. Only the common plants thrived in the high-competition meadow habitat, further suggesting that the rare grassland species are poor competitors. Commonness and rarity are temporal designations that can change as disturbance alters the landscape. Glacial retreat and low precipitation in northeastern N.A. created a landscape suitable for poor competitors that tolerated poor conditions. Our results suggest that rare remnant grassland plants, unlike their close relatives, display more biotic than abiotic limitation as they do not compete well

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with other plants. These results suggest that suitable habitat is not a spatial location but a temporally transient assemblage of species requirements.

Keywords Recruitment · Germination · Community assembly · Grassland · Rarity · Prairie peninsula · Seed limitation

Introduction

Ecological communities typically contain a few common species and lots of uncommon ones (Bevill and Louda 1999; McGill et al. 2007; Preston 1948; Whittaker 1972). What determines commonness and rarity, however, remains an open question (Hubbell et al. 1999; Warren and Bradford 2011). Plant distributions suggest that habitat generalists are common and specialists are rare (Pärtel 2002), but these inferences do not indicate the mechanisms causing the patterning (Pärtel 2002 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 and 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 (Albrecht and McCarthy 2009; Grubb 1977; Warren and Bradford 2011).

Recruitment (seed and seedling survival) is essential for the survival and persistence of plant populations (Eriksson and Ehrlén 1992). Individual plants must replace themselves to maintain populations, or they must establish new populations by dispersing propagules to novel habitats. Whereas recruitment failure in unsuitable habitat hinders colonization, plants also can be seed limited in optimal habitat (Eriksson and Ehrlén 1992; Verheyen et al. 2004). 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 (Clark et al. 2007; Eriksson and Ehrlén 1992; Nathan and Muller-Landau 2000; Turnbull et al. 2000).

Abiotic habitat conditions underlay all plant distributions (Peterson 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 and MacDonald 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. Similarly, 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; Rosenzweig 1981, 1991; Whittaker 1972).

Habitat quality also limits plant species recruitment (Clark et al. 1998, 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 (MacDougall and Wilson 2007; Tilman 1997; Zeiter et al. 2006). 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 increased seed predation by granivores (Brown and Heske 1990; Howe and 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 (Crawley 2000; Edwards and Crawley 1999; Orrock et al. 2006). Moreover, seed predators can eliminate plant species before they have a chance to germinate (Orrock et al. 2006). Additionally, white-tailed deer (*Odocoileus virginianus*) populations are at historically high densities in eastern North America (N.A.) (Garrott et al. 1993), and they often browse specific plant species, which cause considerable changes in plant communities (Rooney and Waller 2003; Stromayer and Warren 1997).

Seed limitation can leave suitable habitat unoccupied (Pulliam 2000) as evidenced by successful experimental introduction of plants into novel habitats (Ackerman et al. 1996; Clark et al. 1998, 2007; Coulson et al. 2001; Crawley and Brown 1995; Eriksson and Ehrlén 1992; MacArthur and MacArthur 1961; Meijden et al. 1992; Piqueray et al. 2013; Primack and Miao 1992). The successful introduction of seeds to unoccupied sites is a strong indicator that the sites were seed and not habitat limited (Piqueray et al. 2013; Primack and Miao 1992).

Glaciation creates large-scale habitat heterogeneity in both space and time (Dupouey et al. 2002; Koerner et al. 1999; Pielou 1991; Ramankutty and Foley 1999). When the glaciers receded from northeastern N.A. (approximately 12,000 B.P.), large deposits of glacial sediment, devoid of plant cover were left behind. Grassland plants initially colonized much of the till after glaciers retreated and formed “prairie peninsula” communities that stretched from western to coastal New York (Transeau 1935; Gordon 1940; Hamilton 2012; York 2013). These habitats persisted for centuries due to a combination of increased temperatures and decreased precipitation during the Holocene Epoch (Gordon 1940; York 2013). 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 and reduces competition for resources light and space for seedlings (Hamilton 2012; Nowacki and Abrams 2008; Steuter 1991). 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) (Hamilton 2012; Overpeck et al. 1992; Pielou 1991). The remaining prairie peninsula communities in northeastern N.A. are remnants of the once extensive distribution (Hamilton 2012).

Approximately 30 % of rare plants (those present in 20–35 extant sites) in northeastern N.A. are remnant prairie peninsula species with fewer than 35 remaining populations (New York Natural Heritage 2013). These same species are abundant in the relatively drier Midwestern (U.S.) habitats east of the Rocky Mountains where drought and fire limit trees and shrubs (Hamilton 2012; Lauenroth 1979; Nowacki and Abrams 2008; Steuter 1991), 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 northeastern N.A. We used seed addition experiments coupled with microhabitat manipulations (burning and herbivore exclusion) in three different habitat types to evaluate recruitment limitation for pairs of closely related congeners of three rare and three common grassland species. If seeds germinated regardless of habitat type or treatment, this would suggest seed limitation. If seeds showed higher germination rates in specific treatment or habitat types, then this would suggest habitat limitation.

Methods

Seedling establishment experiment

Study site

Research was performed at Beaver Meadow Audubon Center, a 151-ha wildlife refuge located in Wyoming County, New York (U.S.) (42.6733°N 78.3846°W). The moderately hilly topography, ranging from 1449 to 1499 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 (Vu Tien 1977). 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 via mowing at the end of the growing season (Vu Tien 1977). No deer control is implemented on site.

Study species

Ontario blazingstar (*Liatris cylindracea*—Asteraceae), sky-blue aster (*Symphotrichum oolentangiensis*—Asteraceae), and giant yellow hyssop (*Agastache nepetoides*—Lamiaceae) are three predominantly Midwestern perennial prairie forb species that have persisted in northeastern N.A. since glacial retreat (Eckel 2001; Nowacki and Abrams 2008). These species are all threatened or endangered in northeastern N.A. (Table 1). Records indicate their current and historical presence in WNY although there are no records of them at the Beaver Meadow site (New York Natural Heritage Program 2014). Boneset (*Eupatorium perfoliatum*—Asteraceae), New England aster (*Symphotrichum novae-angliae*—Asteraceae), and purple giant hyssop (*Agastache scrophulariifolia*—Lamiaceae) are common throughout their range, and grow in similar habitats. *S. 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

Table 1 State ranking system for plant species status in New York State demonstrating the ranking of experimental species (New York Natural Heritage Program 2014)

Species	State rank	Description
<i>L. cylindracea</i> (rare), <i>Symphotrichum oolentangiense</i> (rare)	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>A. nepetoides</i> ^a (rare)	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>A. nepetoides</i> ^a (rare)	S3	Rare in New York state (usually 21–35 extant sites)
<i>A. scrophulariifolia</i> (common)	S4	Apparently secure in New York state
<i>E. perfoliatum</i> (common), <i>S. novae-angliae</i> (common)	S5	Demonstrably secure in New York state

^a The status of some historical populations is unknown since last survey

or endangered. Based on phylogeny, the genus *Eupatorium* is considered the closest *Liatrix* relative in the study area (Schmidt and Schilling 2000) and so *E. perfoliatum* was used as the common comparison species for *L. cylindracea*. Each common species is secure in northeastern N.A. and, although they are present on site, the study locations were surveyed to make sure no populations occurred nearby (Table 1). With the exception of *A. nepetoides*, which prefers moist, rich, open woodland areas (Fernald 1951; Gleason and Cronquist 1991; Toomey and 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 (Corrigan 2002; Young 2010; New York Natural Heritage Program 2014). The three rare species are declining throughout the northeastern United States (Table 1).

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 early April 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 m² ($n = 18$ total). Each grid contained four, 0.5 × 0.5 m treatment plots: burn (burned), deer (deer exclusion), burn + deer and control separated by 0.5 m (Appendix 1). We tested for seed limitation by adding seeds of our study species to each plot. If seeds germinated regardless of habitat type or treatment, this would suggest seed limitation. We simultaneously tested for habitat limitation via microhabitat manipulation. If seeds showed higher germination rates in specific treatment or habitat types, then this would suggest habitat limitation. For the burn treatment, we 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 × 0.5 × 0.5 m PVC frame (secured to the ground with two rebars) covered in bird netting (held to the frame by cable straps) to prevent browse on the study species (MacDougall and Wilson 2007). Treatment type and seed planting location within the grids were selected randomly.

Seeds of *A. nepetoides* were collected from a remnant population 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 natural meadows in Marilla, NY (42.817718°N, -78.501267°W). Seeds were haphazardly collected from individuals from approximately 20 % of each population. Pappi were removed from seeds of *E. perfoliatum* and *S. novae-angliae* following collection. Seeds of *A. nepetoides* did not require any cleaning. Seeds of *L. cylindracea*, *S. oolentangiensis* and *A. scrophulariifolia* were too rare or uncommon to collect, and they were purchased from Prairie Moon Nursery (Winona, MN). These seeds were pre-cleaned by Prairie Moon Nursery before arrival. The seeds were cold stratified at 2.5 °C for two months to break seed dormancy. Stratified seeds of each species were homogenized into species-specific containers. Ten seeds of each were placed in species-specific plastic bags with a tablespoon of potting soil to ensure soil to seed contact upon sowing in early April. Each treatment plot contained 6 subplots (one for each species), and each was planted with 10 seeds of the study species. Bags containing seeds from each species were inverted, emptying the contents into the subplots. The

identity of each species was matched with the subplot so that they could be relocated throughout the growing season. Plots were then covered with a wood fiber seed blanket held down with landscape pins to protect the seeds from granivores and keep them from washing away during heavy rainfall.

All plots were checked twice a week for germination. 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 and averaged for each treatment at the end of the growing season. In early October, when frost marked 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 in order to assess the role interspecific competition for light played in germination and survival of the study species. All of the surrounding vegetation in each treatment except for seedlings of the study species was cut at the level of the soil, placed in a paper bag, and dried in a drying oven for 3 days at 65 °C. After 3 days, plant matter was removed and weighed. Seedlings were defined as the growing stage between germination and the end of the growing season.

Data analysis

Species-level differences in germination (germinated seeds/planted seeds) and survival (surviving seedlings/germinated seeds) were evaluated as binomial proportions using generalized linear models assuming binomial error distributions. The models were fit using Analysis of Deviance (ANODEV) in the R statistical package (R Core Team 2016). Post hoc analyses were conducted using the “multcomp” package (Hothorn et al. 2008). Germination and survival also were evaluated as functions of habitat (forest, meadow, edge), treatment (burn, exclusion, control) and rarity (common, rare) using ANODEV models. Grid identity was included to examine potential block effects, and rarity \times habitat and rarity \times treatment interaction terms were included in the models. We tested for collinearity using the “car” package (Fox and Weisberg 2011). We also tested for overdispersion.

We 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).

We considered coefficients with $p < 0.05$ as significant and $p < 0.10$ as marginally significant (sensu Hurlbert and Lombardi 2009).

Results

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).

Table 2 Average environmental parameters (\pm SE) for each habitat type

	Meadow	Edge	Forest
Soil moisture (%)	27.08 \pm 0.41	25.57 \pm 0.36	24.32 \pm 0.32
Soil temp. ($^{\circ}$ C)	18.80 \pm 0.06	17.48 \pm 0.02	17.40 \pm 0.04
PAR (%)	46.76 \pm 1.77	4.48 \pm 0.62	3.22 \pm 0.12

Germination success differed marginally significantly between study species ($df = 5$, $p = 0.073$). 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 ($p = 0.042$) (Fig. 1). None of the study species had average germination rates >5 %.

Germination was not affected by habitat type ($\chi^2_2 = 4.164$, $p = 0.124$), but was influenced by transect ($\chi^2_2 = 23.23$, $p \leq 0.001$) as transect 1 had twice the germination (6.8 %) as any other transect. A significant treatment \times rarity interaction term ($\chi^2_2 = 10.478$, $p = 0.015$) indicated that rare species germination 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 germination was greater than rare species germination in exclosure treatments (rare = 1.30 \pm 0.53, common = 3.15 \pm 0.95) (Fig. 2). All species germination was greater in the burn and burn + exclosure treatments than the control plots (Fig. 2).

We only found an estimable fitted line for the influence of biomass on rare plant germination at the 99th quantile ($coeff. = -125$, $SE = 55.566$, $t = -2.237$, $p = 0.026$) (Fig. 3a). Conversely this was not the case for common species ($coeff. = 0$, $SE = 113.841$, $t = 0$, $p = 1$). Only rare species germination was limited by biomass density (Fig. 3b).

Survival did not differ significantly ($df = 5$, $p = 0.147$) between study species and was not greater than 15 % overall. It also was not affected by transect ($df = 5$, $p = 0.194$), but did differ by treatment ($df = 3$, $p = 0.017$) as no plants survived in the control plots and mean survival for the treatments was: burn 4.167 % \pm 3.069, exclusion 2.941 % \pm 2.941,

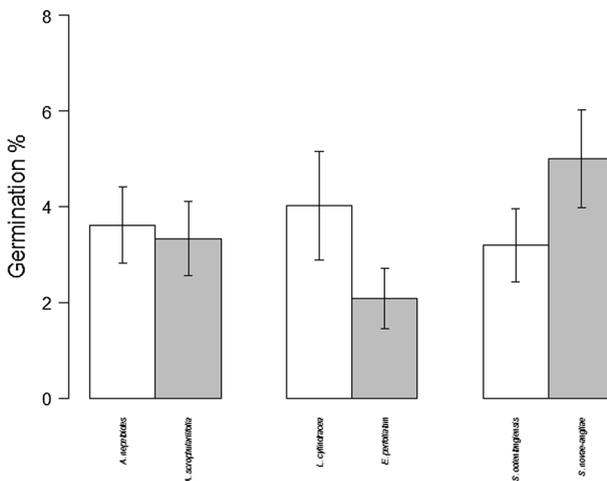


Fig. 1 Mean (\pm SE) germination rates (%) for each species of rare (white) and common (gray) grassland species. Only the germination rates of *L. cylindracea* and *E. perfoliatum* differed significantly

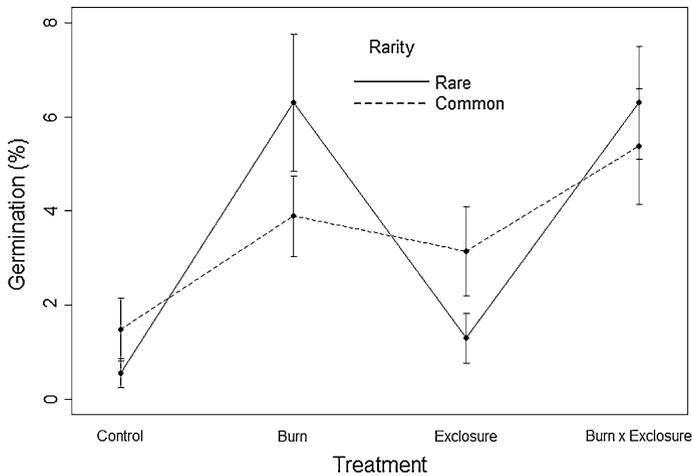


Fig. 2 Interaction plot showing mean (\pm SE) % germination across experimental treatments. Rare species germination was significantly higher than common species in the burn treatments whereas common species germination was significantly higher than rare in the exclosure treatments. Both rare and common species germination was higher in treatments that included burning

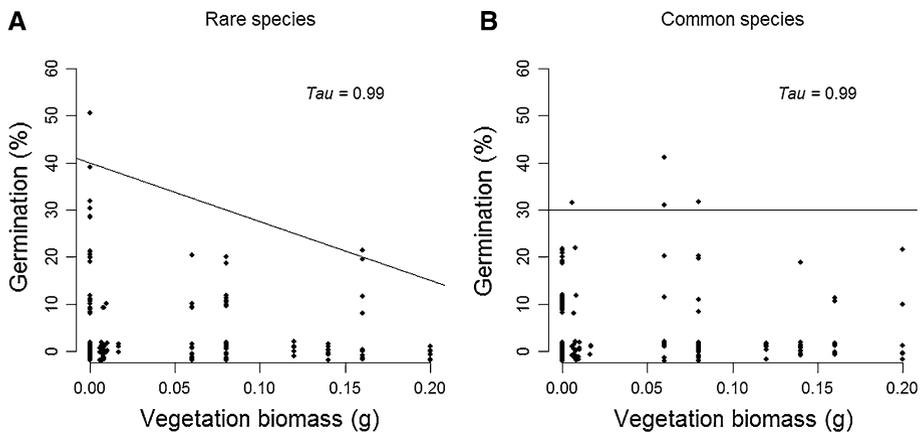


Fig. 3 Quantile regression indicating that interspecific biomass set the upper limits on rare species germination (a) but not common species germination (b) at the 99th quantile

and burn + exclusion $17.063\% \pm 5.637$. A significant habitat \times rarity interaction term ($df = 2$, $p = 0.041$) 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. scopulariifolia* = 0% , *S. novae-angliae* = 0%), but common species survived much better in meadow habitat (*L. cylindracea* = $8.3\% \pm 0.58$, *A. nepetoides* = 0% , *S. oolentangiensis* = 0% , *E. perfoliatum* = 0% , *A. scopulariifolia* = $8.3\% \pm 0.58$, *S. novae-angliae* = $8.3\% \pm 0.58$) than rare species (no survival) (Fig. 4).

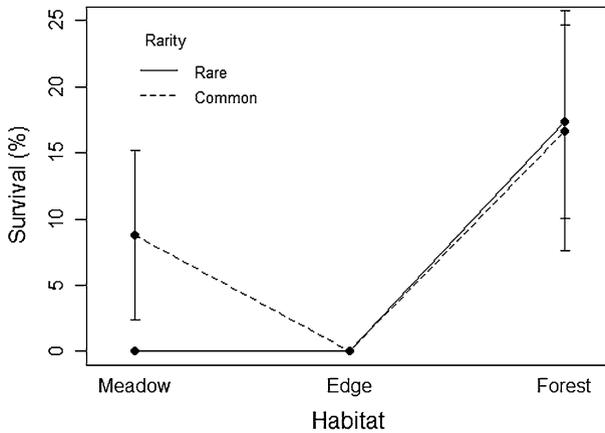


Fig. 4 Habitat interaction plot showing mean (\pm SE) % survival. Both rare and common species survived equally poorly in edge habitat and equally better in forest habitat, but the common species survived significantly better in the meadow habitat than the rare species

Discussion

Rarity of remnant grassland plant species in WNY is more a function of habitat limitation rather than seed limitation. Rare grassland species do not compete well with common plants in the absence of disturbance. 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.

Disturbance plays a considerable role in plant community assembly (White and Jentsch 2004). Burning increased germination, especially for the rare grassland species, as it does for grassland species worldwide Briggs et al. (2002, 2005; Brockway et al. 2002; Collins and Barber 1986; Harrison et al. 2003; Waldrop et al. 1992). Seedling establishment decreases with species richness in grassland habitats (Tilman 1997). The poor overall performance of the rare species suggests that seed limitation plays a relatively small role in the limited distribution of these species. Instead, 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 and Grace 2002), confirming 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 (Nowacki and Abrams 2008; Steuter 1991).

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 and 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 (Ratajczak et al. 2011; Van Auken 2009), 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 significantly 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 none survived in the 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 N.A. 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 if the plants can persist—particularly as grassland species reproduction often is limited by shading (McKinney and Goodell 2010). Although survival in the first season is a crucial bottleneck that plant species must overcome in order to survive in a given habitat, plants must also be able to grow and survive beyond the seedling stage in order for persistent populations to form. Despite germination and growth in the forest habitats, it is not likely given the ecology of grassland species, that long-term survival in such a habitat would be likely. As such, a measure of growth and reproductive output is needed to determine the success of these species in each habitat type. This can only be achieved through long-term investigation.

Seed source can have important effects on germination and survival (Galloway 2005; Bischoff et al. 2006; Gallagher and Wagenius 2016). As such, we cannot discount the effects of seed sources on germination and survival of our study species. Whereas we were able to collect seeds of *A. nepetoides*, *E. perfoliatum*, and *S. novae-angliae* from natural populations in WNY, the protected status and small population sizes of *L. cylindracea* and *S. oolentangiensis* as well as the absence of *A. scrophulariifolia* from the immediate study area meant that we had to purchase seeds from outside the area. The low germination rates may have cost our study design some statistical power, but the germination rates were high enough for detectable statistical patterns. Moreover, the statistical power gained by adding seeds would be somewhat misleading as the seed additions are clustered and hence highly autocorrelated. Beyond statistical considerations, even though individual plants may release copious amount of seed, the number of seeds falling in a single spot likely will not be high, making our study design realistic for natural conditions. Moreover, propagule pressure can overwhelm habitat filtering so that using copious amounts of seed compromises the evaluation of habitat limitation (Warren et al. 2012).

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, seed 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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Appendix 1

See Fig. 5.

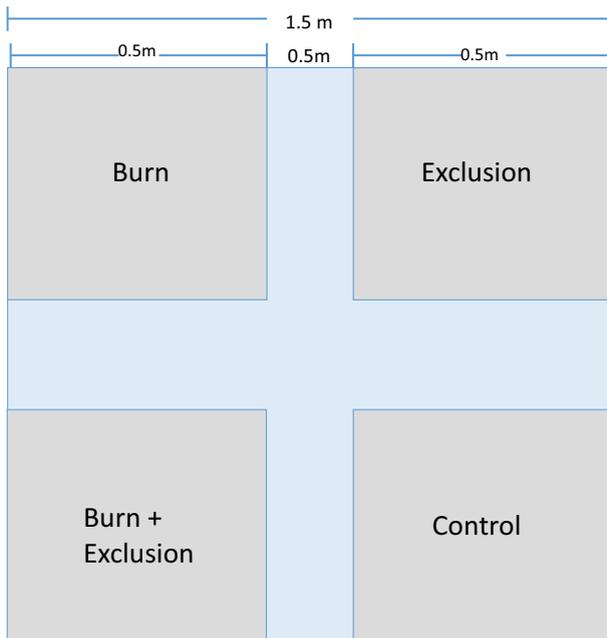


Fig. 5 Treatment grid design for experimental burning (burn) and herbivore exclusion (exclusion)

Appendix 2

See Table 3.

Table 3 Statistical ANODEV results for germination and survival of study species for the seed addition experiment

Source of variation	Germination			Survival		
	<i>df</i>	χ^2	<i>p</i> value	<i>df</i>	χ^2	<i>p</i> value
Block	5	23.23	0.000305*	5	23.591	0.0002602*
Habitat	2	4.164	0.124688	2	4.137	0.1263708
Treatment	3	55.181	<0.001*	3	54.847	<0.001*
Rare	1	0.062	0.802887	1	0.062	0.8037082
Habitat:rare	2	0.508	0.775755	NA	NA	NA
Treatment:rare	3	10.478	0.014910*	3	10.467	0.0149885*

The table shows degrees of freedom (*df*), Chi Square (χ^2), and *p* value. Values with * are significant at alpha ≤ 0.05

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