1 Habitat change in insular grasslands: woody encroachment alters
2 the population dynamics of a rare ecotonal plant
3
4

5 Matthew A. Albrecht^{1*}, Rachel Becknell², and Quinn Long¹
6
7

8 ¹*Center for Conservation and Sustainable Development, Missouri Botanical Garden, St.*
9 *Louis, MO, USA, 63166*
10

11 ²*Department of Biology, Washington University, St. Louis MO, USA, 63130*
12

13 *Corresponding author: Tel: +1 314 577 0262; fax: +1 314 577 0847
14 matthew.albrecht@mobot.org
15

16
17 *Keywords:* landscape matrix; succession; cedar glades; management; habitat suitability;
18 disturbance
19

ABSTRACT

Inferring habitat requirements of rare plants can be challenging when the few remaining populations occur in sites with divergent successional states. In island-like rock outcrop systems within forest landscapes, edaphic conditions are assumed to modulate successional patterns, but changes to disturbance regimes in the landscape matrix could alter ecotone microenvironments over time. We used demographic surveys and controlled experiments with a dispersal-limited and endangered ecotonal plant, *Astragalus bibullatus*, to test the hypothesis that woody encroachment from the forest matrix threatens rare plants in globally imperiled limestone cedar glades. Tree canopy cover was more important than edaphic conditions or ground-layer structure for explaining variation in demographic structure. As tree canopy cover increased, stem densities, flowering, and seed production declined. Over three-years, per plant inflorescence production, fruit production, and fruit set were markedly greater in open microhabitats than in edge or closed microhabitats. In contrast, seedling densities peaked in edge and closed microhabitats. Seedling recruitment and seed production were spatially decoupled across a canopy cover gradient, suggesting that shaded sites historically had lower tree canopy cover. Shade reduced growth rates and biomass of seedlings and adults under non-limiting moisture conditions. Although *A. bibullatus* can persist in degraded ecotones using multiple demographic strategies, growth, flowering and seed production depend on open microhabitats. Our results demonstrate that woody encroachment effects in temperate grasslands extend to island-like rock outcrop systems with unique edaphic conditions. Conservation and recovery programs with rare ecotonal plants should integrate restoration of historical disturbance regimes in the landscape matrix.

1. Introduction

Habitat degradation caused by altered disturbance regimes is a principle threat to the long-term persistence of rare plant populations (Hobbs and Huenneke 1992; Jules and Shahani 2003; Williams et al. 2006). Altered disturbance regimes, such as changes in fire frequency, human land-use, and management practices, can directly influence rare plant populations by altering microsite availability, vegetation structure, soil fertility, and biotic interactions (Brys et al. 2005; Menges and Dolan 1998; Middleton 2013; Vitt et al. 2009). Because rare species with restricted distributions often depend on periodic disturbances to create suitable habitat, a major challenge for conservation is to understand their response to habitat change and successional processes (Jolls et al. 2015; Menges and Quintana-Ascencio 2004; Pardini et al. 2015).

In patchy habitats, rare ecotonal plants might be especially vulnerable to altered disturbance regimes, because conservation management tends to focus on dominant community types or distinct habitat patches (e.g., rock outcrops) in the prevailing landscape (Kark 2013). Rare species can be restricted to ecotones because they require environmental conditions intermediate to adjacent habitats or specialize on distinctive microhabitats within the ecotone (Lloyd et al. 2000; Odum 1983; Risser 1995). However, periodic disturbances (e.g., fire) can shift ecotones across space and time, making it difficult to distinguish ecotone boundaries and infer species habitat preferences (Possley et al. 2008; Risser 1995). For example, disturbance-dependent rare plants can persist in suboptimal conditions during disturbance-free intervals via seed banks or vegetative reproduction (Colling and Matthies 2006; Menges and Dolan 1998). Rare ecotonal species can also persist in human-altered habitats where modern-day disturbances mimic

historical disturbance regimes (Clarke and Patterson 2007; Pavlovlic 1994; Quintana-Ascencio et al. 2007), which once maintained suitable habitat that may now be degraded or have vanished entirely (Fowler et al. 2012; Possley et al. 2008).

In this study, we ask whether altered disturbance regimes influence rare ecotonal plants in limestone cedar glades (LCGs) of the southeastern United States (U.S.), where edaphic conditions, rather than disturbance, have long been considered the primary factor controlling vegetation structure (Baskin et al. 2007; Baskin and Baskin 1999). LCG's are natural-habitat islands of rocky and infertile soils that support communities dominated by small-statured, heliophytic C₃ grasses and annual forbs, including many rare and endemic species (Baskin and Baskin 1999). Considered a globally imperiled ecosystem and hotspot of plant endemism in the Southeastern U.S. (Estill and Cruzan 2001), LCG ecosystems have declined by 90% since Euro-American settlement (Noss et al. 1995), while ongoing and widespread urbanization severely fragments remaining LCGs (Bowen 2011). LCG's are considered stressful habitats, characterized by exposed rock pavement, nutrient-poor and thin soils, and seasonal microclimate extremes, which can impede establishment of woody vegetation (Baskin et al. 2007; Baskin and Baskin 1999). Glade ecotones are typically very narrow and markedly abrupt transition zones between open glade and surrounding forest, with deeper pockets of soil that support perennial forbs and C₄ grasses. Rare perennial forbs restricted to these ecotones often occur in small, declining populations (Albrecht and McCue 2010; Sutter et al. 2011; Thompson et al. 2006), and tend to be intolerant of the drought-prone open rock outcrops (Baskin and Baskin 2005).

Woody encroachment poses a major threat to grassland, savanna, and open woodland ecosystems globally (Bond and Midgley 2000; Briggs et al. 2005; Van Auken 2000). In North American grasslands, changes in fire frequency have facilitated woody encroachment (Ratajczak et al. 2014), which fragments remnant habitats and reduces herbaceous diversity (Alofs and Fowler 2012; Ratajczak et al. 2011a). Although LCG ecotones are presumably maintained by locally abrupt changes in edaphic conditions (Baskin and Baskin 1999; Quarterman 1950a; Ware 2002), several lines of evidence suggest woody vegetation is expanding into rock outcrop systems and shrinking ecotone habitat. The abundance of fire-sensitive, mesophytic tree species is increasing in forests adjacent to LCGs (Adams et al. 2012), and long-term declines in the abundance of LCG endemics are associated with recent increases in woody cover, especially *Juniperus virginiana* L. (commonly known as eastern red cedar; hereafter 'cedar'; Sutter et al. 2011). Evidence of reduced gene flow and genetic variation over time in the focal species of this study further suggests that these island-like outcrops were historically connected by a more open landscape matrix (Morris et al. 2002). However, because little is known about the spatial and temporal dynamics of LCG ecotones, there is an urgent need to determine optimal habitat conditions and appropriate management strategies to conserve globally imperiled species restricted to glade-forest ecotones.

To test the hypothesis that rare species in LCG ecotones are threatened by woody encroachment, we examined environmental drivers of demographic structure across a woody cover gradient for an endangered herbaceous perennial, *Astragalus bibullatus* Barneby & E.L. Bridges. Our approach is based on previous work demonstrating that demographic structure of long-lived perennials provides a snapshot of past habitat

conditions, which can indicate how changing environmental conditions influence plant populations (Doak and Morris 1999; Endels et al. 2004; Gotelli and Ellison 2002). If rare ecotonal species require disturbances in the matrix to maintain open ecotone conditions, then we predict that tree cover is the most important determinant of demographic structure, and we expect declines in demographic performance as microhabitats become closed by woody vegetation. Alternatively, if rare ecotonal species prefer late-successional conditions typical of shaded glade ecotones, then we expect greater demographic performance in narrow glade-forest edges relative to open, early-successional microhabitats maintained by disturbance.

2. Material and Methods

2.1. Study species and system

Astragalus bibullatus is a small-statured (up to 15 cm tall), nitrogen-fixing, perennial legume (Baskin and Baskin 2005). Listed as globally critically imperiled (G1 rank, NatureServe), the species is known from < 5000 individuals, a majority of which occur in distinct patches in a 90 km² area (USFWS 2011). Most plants begin flowering in early-to-mid spring (April-May), before deciduous tree leaf-out, and produce mature legumes in late-spring (May-June). Seeds are gravity dispersed and can remain viable in the soil for decades (Morris et al. 2002). However, little is known about factors influencing the ecology and population dynamics of *A. bibullatus* (Baskin and Baskin 2005), which are essential for recovery efforts and adaptive management actions to ensure this species' survival in the wild (USFWS 2011).

A major challenge for inferring habitat preferences of *A. bibullatus* is that the few known naturally occurring populations are numerically small, occur in sites with divergent successional states, and have different management histories (mowed vs. unmowed). Because of these challenges, we used demographic surveys coupled with experiments to test the hypothesis that demographic performance declines with increasing woody vegetation cover. First, we determined the relationships between demographic structure and microhabitat variation in patches of *A. bibullatus* that were distributed across a gradient of tree canopy cover generated by mowing and natural succession. Second, we examined the demographic performance of seedlings and reproductive adults in open, edge, and closed sites. Third, we subjected seedlings and adult plants in a pot experiment to seasonal (spring and summer) light regimes that reflect varying degrees of woody encroachment. We focus on adults and seedlings in the latter two studies because initial surveys indicated that some sites support seedlings but not reproductive adults, and vice versa.

2.2. Demographic structure and ecological gradients

We sampled all six naturally occurring protected sites using permanently marked 1 m² plots ($n = 22$). A seventh site occurred on private property and was not sampled. Two adjacent sites have been maintained ($n = 10$ plots) by mowing during the late growing (after plants fruit) or dormant season (~3 every years, personal communication, D. Lincicome, Tennessee Department of Environment and Conservation), although no sites were managed during this study. These two open sites maintain the largest concentration of *A. bibullatus* plants (~1000 plants) and support populations of other

LCG endemics. Other than a few large chinkapin oaks (*Quercus muehlenbergii* Engelm.) and cedars scattered throughout the area, densities and cover of woody vegetation are low due to long-term periodic mowing. All other sites sampled in the study have persisted for > 15 years without mowing or other management. Populations at three unmowed sites are located in narrow ecotones between shallow-soil, rocky openings and the forest matrix dominated by cedar. The number of plots established at each edge site depended on population size, with the greatest number of plots ($n=8$) established at the largest (~500 plants) edge site, two at sites with < 50 plants, and two at a site containing two distinct, small patches of plants (< 20 plants). At each site, we established plots in dense patches of *A. bibullatus* that varied in the amount of tree canopy cover (range 13-88%).

From 2010 to 2012, we quantified five demographic structure variables in each plot during peak fruiting, including densities of seedlings, multi-stem vegetative adults, and flowering adults. Seedlings were classified as 1-stem plants with a stem length ≤ 5 cm. For each adult plant, we recorded the number of stems and fruits. Percent cover was estimated visually within each plot for the following variables each spring: forbs, graminoids, mosses, woody plants, broadleaf litter (forb and tree litter), graminoid litter, bare ground, and exposed rock. Tree canopy cover was quantified in each plot using a convex spherical densiometer following the protocol of Lemmon (1956). In each plot, we quantified average soil depth using a metal rod inserted to the depth of bedrock within each of four $0.5\text{ m} \times 0.5\text{ m}$ quadrants. In June 2010, two soil cores ($10\text{ cm} \times 10\text{ cm} \times 5\text{ cm}$ deep) were collected immediately adjacent (< 20 cm) to each plot and combined into a composite soil sample for that plot. Soil moisture and soil chemistry (pH, organic

matter, NO₃, NH₄, P, Mg, Ca, K, and CEC) were quantified using standard methods (see Supplementary Material).

We used Principle Components Analysis (PCA) and redundancy analysis (RDA) in the vegan package (Oksanen et al. 2015) to examine differences in microhabitat variation among mowed ($n = 10$) and unmowed plots ($n = 12$). A PCA was conducted on 15 microhabitat variables, including nine percent cover variables, two soil variables (depth and moisture), and a subset of soil chemistry variables (pH, CEC, NO₃, and P). The latter were identified in a preliminary PCA (see Table S1). We used the broken stick method (Borcard et al. 2011) to determine that the first two principle components (PCs) described significant amounts of microhabitat variation among open and edge plots. We report results from a PCA where environmental predictors were averaged over a three-year period (2010-2012), since separate PCA's for each year would have included only a subset of the variables.

We used RDA to examine whether demographic structure covaried with microhabitat. Because most demographic variables did not vary among years (see below), we used cumulative plot averages across years for each demographic variable (log-transformed) and 15 microhabitat predictors, including habitat management (mowed vs. unmowed). To minimize the influence of multicollinearity, we first fit a full RDA model and then used a forward model selection procedure based on permutation tests and Akaike Information Criterion (AIC) values to determine the most parsimonious RDA model (Borcard et al. 2011). We examined the significance of microhabitat variables and RDA axes using permutation ANOVAs ($n = 999$), and compared the importance of

microhabitat predictors based on their significance in the full and reduced model (Borcard et al. 2011).

To examine the relative importance of microhabitat variables on demographic performance, we used generalized linear models with a negative binomial distribution and AIC_c , adjusted for small sample size. We fit separate models for each combination of demographic variable and year (hereafter, ‘model set’). Using information theoretic approach for model selection, we used the package MuMIN (Kamil 2015) to evaluate combinations of models (including a null model) that included a subset of the 15 microhabitat variables (see above), chosen *a priori* based on their significance in the RDA (see below), and the expectation that light, vegetation cover, and soil depth are the primary factors influencing rock outcrop endemics (Baskin and Baskin 1988). Each model set included five microhabitat predictors (soil depth, canopy, forb, grass, and litter cover), and two soil chemistry variables (NO_3 and CEC) were included in the 2010 analysis only. To avoid overfitting, we did not allow more than five parameters (including intercept) to enter each model and we only examined additive effects. To minimize the influence of multicollinearity, we prevented combinations of microhabitat variables that were significantly correlated from entering the same model. To select models that best approximated the data, we used model weights (w_i) and the relative difference (ΔAIC) to the smallest AIC in each model set (Burnham and Anderson 2002). We report top ranked models with AIC_c differences ($\Delta_i = AIC_i - AIC_{min}$) less than or equal to two ($\Delta_i \leq 2$) (Burnham and Anderson 2002). We standardized each predictor to facilitate comparing the relative importance of microhabitat variables (Schielzeth 2010).

To examine how demographic structure varied over time and among habitats we used generalized linear mixed models (GLMM, negative binomial distribution) in the `gamm4` package (Wood and Scheipl 2014). We fit separate models for each demographic variable, with each model incorporating plot as a random intercept and year as a random slope. All analyses were conducted in R 3.21 (R Core Team 2015).

2.3. Recruitment and tree canopy cover

To better understand vital rates underlying differences in demographic structure, among sites, we demographically surveyed seedlings and adult plants at sites that varied in tree cover. At the mowed (hereafter ‘open’, 14% canopy cover) and unmowed (hereafter ‘edge’, 49% canopy cover) sites with the largest population sizes, we established a 30 and 20 m long transect, respectively, through the population core and tagged up to 30 reproductive adult individuals in 2010. The unmowed site (hereafter ‘closed’) with the highest canopy cover (88%) is a narrow (3-4 m wide) rocky opening in a cedar-hardwood forest. We established an 8 m transect in the opening and tagged a majority of the plants ($n = 35$), including all adults. Each spring we tagged up to 30 new seedlings at each site and followed their survival and growth over the three-year period. For three years, we followed the fate of reproductive adults tagged in 2010, adding reproductive adults to the dataset to compensate for mortality ($< 10\%$) as needed. For reproductive adults, we counted the number of inflorescences, number of infructescences (inflorescences with ≥ 1 fruit), and total number of fruits. In 2011 and 2012, we subsampled fruits from up to 30 randomly selected individuals per population and determined the number of viable seed per fruit, based on the firmness and color of seeds

(Albrecht and Penagos 2012). We used generalized linear mixed models (GLMM's) to examine differences among habitats in first-year seedling survival (binomial distribution), per plant inflorescence production (negative binomial distribution), number of seeds per fruit (negative binomial distribution), and per plant fruit set (binomial distribution). When main effects were significant, we used Tukey pairwise comparison tests in the lsmeans package (Lenth and Herv 2014). Because reproduction and seedling recruitment were low in some years, we pooled data over the three years. The closed site was not included in the analysis of fruit set and number of seeds per fruit, due to low fruit production.

2.4. Pot study

Because natural population surveys showed that seedlings and adults responded differently to woody vegetation cover, we used a fully randomized design to manipulate seasonal light regimes that simulate the presence (CE^+) and absence (CE^-) of cedar. For CE^- treatments (0% spring cover), we varied summer light conditions to mimic deciduous tree canopy cover: open (OP^- , 0% summer cover), open woodland (OW^- , 50% summer cover), and closed woodland (CW^- , 75% summer cover). To mimic shade cast by cedar encroachment, we added both spring and summer shade to the CE^+ treatments: OP^+ (50% spring and summer cover), OW^+ (50% spring and 75% summer cover), and CW^+ (75% spring and summer cover). The CW^+ treatment mimics light conditions of a closed cedar forest that surrounds most LCG outcrops (Adams et al. 2012). We used one and two layers of 50% shade cloth to achieve the desired canopy cover of 50% and 75%, respectively. Light levels quantified (PAR meter; Apogee Instruments ®) below and above shade structures indicated that the 50% and 75% cover treatments had 52.6% ($\pm$

1.06 SE) and 73.6% ($\pm$ 0.87 SE) average light interception, respectively. To simulate full leaf out of a deciduous canopy in early summer, shade cloth was added to woodland treatments (OW⁻, CW⁻, and OW⁺) two months after the start of the experiment.

In April (2014), we established 36 plots (n = 6 plots per light regime) at a common garden located in full sun at the Missouri Botanical Garden's Shaw Nature Reserve. Six pots containing *A. bibullatus* seeds (n = 3) and vegetative adults (n = 3) were established in each plot. In each seed pot, we sowed two non-dormant seeds (previously scarified in 90% H₂SO₄ and stratified at 5°C for 4 weeks), whereas each transplant pot contained a single plant. All plant material used in the experiment was sourced (2012) from the mowed/open site with the largest population. Transplants (vegetative adults, ~1-year old) were grown from seed and kept in pots outdoors in the open under constant moisture. One month after sowing, seedlings from pots with two germinants were transplanted to pots in which no seeds had germinated. Throughout the experiment, pots were watered to maintain constant moisture and all plants were treated with a fungicide (Physan 20 ®) to control powdery mildew. Every two weeks (May – October, 2014), we recorded emergence, number of stems, and diameter of each surviving seedling and adult. To minimize destructive sampling of an endangered plant, we randomly subsampled five individuals in the OP⁻, OP⁺, and CW⁺ treatments at the end of the experiment, and recorded above and belowground biomass. The roots and shoots were separated from each plant and dried at ~40°C for 72 hours.

Because preliminary analyses indicated no differences in response variables among light regimes within the CE⁺ and CE⁻ treatments, we pooled data for each of the three CE⁺ and three CE⁻ light regimes. We used separate GLM's to test for differences

among CE⁺ and CE⁻ treatments in germination (binomial error), final survival (binomial error), final stem number (Poisson error), relative growth rate (calculated as log difference in diameter in the last October census and the first June census divided by the elapsed time in days), total biomass, root mass, and shoot mass, and root:shoot ratio. None of the transplants flowered during the study. For RGR and biomass measurements, we used a Gaussian error distribution. To avoid pseudoreplication, mean values were calculated for each plot by averaging across individuals that survived to the last October census. We conducted separate analyses for seedlings and transplants.

3. Results

3.1. Microhabitat variation and demographic structure

The first two PCs explained 49% of environmental variation among plots, with mowed and unmowed sites separating clearly along PC1 (Fig. 1a). Mowed plots tended to have a greater forb cover, litter cover, and soil NO₃ than unmowed plots, while the latter had greater moss cover, grass cover, and soil moisture (Fig. 1b; Table S2). Although tree canopy cover separated microhabitats along PC2 ($r = -0.65$, $P < 0.0001$) more than PC1 ($r = 0.30$, $P = 0.15$), canopy cover (logit transformed) was significantly lower in the mowed relative to unmowed site (GLM, $F_{1,20} = 5.00$, $P = 0.037$, Fig. 1c). In the full RDA model, habitat and forb cover were the only microhabitat variables explaining significant variation in demographic structure (Table 1). The reduced RDA model contained two significant axes (RDA1: $P = 0.001$, RDA2: $P = 0.004$), three predictors, and explained 41.0% (adjusted R^2) of the variance in demographic structure among plots. Of the significant predictors, canopy cover explained almost half the

variance in demographic structure (Table 1). Because habitat exhibited the highest variance inflation factor (VIF) among predictors and covaried with predictors in the reduced model, suggests differences in demographic structure among habitats can be largely attributed to microhabitat differences generated by variation in tree canopy cover. Seedling recruitment was orthogonal (unrelated) to fruiting in the RDA biplot (Fig. 1d), implying spatial discordance between these two demographic processes. Seedling recruitment occurred in microhabitats with low forb cover, whereas fecundity was strongly correlated with microhabitats exhibiting low canopy cover (Fig. 1d). Seedling densities were significantly greater in unmowed than mowed plots ($F_{1,55} = 12.64$, $P < 0.001$, Fig. 2a), whereas plants in mowed plots produced more stems per adult ($F_{1,55} = 25.26$, $P < 0.0001$, Fig. 2b), reproductive adults ($F_{1,55} = 4.07$, $P = 0.047$, Fig. 2c), and legumes ($F_{1,55} = 6.10$, $P = 0.01$, Fig. 2d). Differences in stage densities among habitats remained consistent among years (habitat $\times$ year: P -values > 0.22)

Similar to the RDA, the most parsimonious regression models indicate that canopy cover and forb cover are the most important predictors of demographic structure (Table 2). Forb cover was a significant predictor of seedling densities in all years (Table 2), and occurred in every top ranked model for 2011 and 2012 (Table S3). Soil N, soil depth, and grass cover were also significant predictors of seedling densities in some years (Table 2 and S3). Seedling densities declined as forb cover, soil N, and soil depth increased (Fig. 3), and increased as grass cover (2010 only) increased (Table 2). Canopy cover was the strongest predictor of stem number, reproductive adult densities, and legume production, appearing in nearly every top ranked model for these variables

(Tables 2 and S3). As canopy cover increased, stem number, reproductive adult densities, and legume production significantly declined (Fig. 3).

3.2. Demographic surveys of seedlings and adults

Demographic stage proportions differed among habitats, as the proportion of reproductive adults increased from closed to open sites whereas the proportion of seedlings declined (Fig. 4a). Greater seedling survival (pooled over three cohorts, P -values < 0.0001) in the closed relative to edge or open sites help explain this pattern (Fig. 4b). Over the three-year period, however, flowering ($n = 6$ plants) and fruiting rates ($n = 8$ fruits in total) were low at the closed site. In contrast, reproductive plants at the open site produced more inflorescences ($P < 0.001$) and greater numbers of fruits ($P = 0.06$) than the edge and closed sites (Fig. 4c). Fruit set was significantly greater in the open than the edge site ($P = 0.008$, Fig. 4d), but there were no differences in the number of seeds per fruit ($P = 0.63$, data not shown).

3.3. Pot study

Overall, 47% of *A. bibullatus* seeds emerged and 70% of seedlings survived during the experiment. Seedling emergence rates were similar in the CE^+ and CE^- treatments ($P = 0.54$), but seedling survival was marginally greater in the CE^- treatment ($P = 0.07$, Fig. 5a). Of the 108 adult transplants, 96% survived during the experiment with no differences among treatments (Fig. 5a). Seedling relative growth rates (RGR) were similar among treatments ($P = 0.79$), but transplant RGRs were significantly greater ($P = 0.01$, Fig. 5b) in CE^- . Overall, fewer stems were produced in the CE^+ relative to the

CE⁻ treatments (Fig. 5c), but trends were more pronounced in seedlings ($P = 0.001$) than transplants ($P = 0.10$). Root mass and shoot mass in both seedlings (P -values < 0.01) and transplants (P -values < 0.001) were significantly greater in the CE⁻ relative to the CE⁺ treatment (Fig. 5d-e). Plants allocated more biomass to roots than shoots, resulting in root:shoot ratios that were greater in CE⁻ relative to the CE⁺ treatment (Fig. 5f).

4. Discussion

4.1 Microhabitat and demographic structure

Multiple lines of evidence indicate that woody vegetation modulates the demographic performance of a rare ecotonal plant. The demographic structure of *A. bibullatus* shifted from small, non-reproductive plants in unmowed sites with high tree canopy cover to larger plants with high fruit production in sites maintained open by mowing. Canopy cover had a stronger effect on demographic structure than edaphic conditions or ground-layer structure, and drove differences in *A. bibullatus* performance among mowed and unmowed sites. Growth and reproduction appeared to be sensitive to light-availability, as stem densities, flowering rates, and fruit set declined with increasing tree canopy cover. In the pot study, growth rates and biomass increased with light-availability and plants exhibited root:shoot allocation patterns consistent with an early-successional plant adapted to high-light conditions (Crawley 1997). Collectively, these results support the hypothesis that woody encroachment negatively impacts the demographic performance of a rare ecotonal plant by altering abiotic and biotic conditions.

Along with a high-light requirement (Baskin and Baskin 1988), endemics of open rock outcrops are assumed to be poor competitors due to a trade-off with stress-tolerance (Lavergne et al. 2003; Quarterman 1950a). In other studies with LCG endemics, local abundance declined with increasing vegetation cover (Thompson et al. 2006), and plant performance in controlled experiments declined with increasing competition from LCG generalists (Baskin and Baskin 2005; Hemmerly 1986). In our study, open microhabitats harbored a greater abundance of high-light-demanding forbs, which significantly influenced demographic structure of *A. bibullatus* by negatively impacting seedling densities, but not flowering or seed production. This finding is consistent with previous studies in successional grasslands that found seedling recruitment in short-statured perennials declined as taller vegetation increased during disturbance-free intervals (Colling and Matthies 2006; Colling et al. 2002; Schleuning and Matthies 2009). The higher concentrations of soil nitrogen in mowed versus unmowed sites (see Fig. 1b) might have further interacted with forb cover to limit *A. bibullatus* seedling establishment. For example, rare species can be outcompeted by common species when productivity and soil nutrients increase (Dawson et al. 2012), and rare nitrogen-fixing legumes tend to maintain competitive advantages only when soil N is limiting (Skogen et al. 2011; Suding et al. 2005).

Differences in seedling recruitment patterns between mowed and unmowed sites also may reflect tree canopy cover effects on resource availability. At the unmowed site with the greatest canopy closure ('closed' site), higher soil moisture coupled with less competition from taller forbs may help explain the greater seedling survival there relative to open or edge sites, especially since a moderate to severe regional drought occurred

during the spring of 2012 (NOAA 2013). In open rock outcrops, evapotranspiration rates can routinely exceed the permanent wilting point during the growing season, and previous studies found that droughts reduced seedling establishment in other LCG endemics (Baskin and Baskin 1989, 1999). In the *A. bibullatus* pot study where moisture and competition were non-limiting, seedling survival and RGR were similar in high and low light environments, although shade did reduce root and shoot mass relative to plants grown in full sun. This suggests that microsite limitation, mediated by tree canopy cover, is an important control on the local abundance of *A. bibullatus*, and that seedlings probably transition to reproductive adults only under a narrow range of microenvironmental conditions (high light, sufficient moisture, and low herbaceous cover).

4.2 Forest edge or degraded ecotone?

Because of their unique edaphic conditions, LCG outcrops with thin soil are relatively stable over long-time scales and succession was not considered a major threat to the endemic flora (Baskin et al. 2007). Consequently, conservation of LCGs has largely focused on the protection of remaining rock outcrops rather than managing woody succession in ecotones and the landscape matrix. However, the spatial decoupling of seedling recruitment and seed production in *A. bibullatus* suggest LCG ecotones historically contained lower tree cover. In the shadiest microhabitats, few plants flowered and fruited over the course of three years, although high seedling densities suggest these microhabitats were not seed-limited. In *A. bibullatus*, seeds are gravity dispersed with no known secondary dispersal agents (Baskin and Baskin 2005) and seeds rarely (<10%)

germinate the first few years after dispersal (Albrecht and Penagos 2012), making it unlikely that recent dispersal events from nearby (< 1 km) open sites explain the seedling recruitment patterns we observed. Instead, a previous study showed that all of the sites sampled here maintain a soil seed-bank that persists for several decades (Morris et al. 2002). Paradoxically, the closed site has the smallest population size and poorest seed production relative to the other sites, yet maintains the greatest soil seed-bank densities (Morris et al. 2002). For this shaded site to accumulate dormant soil seed pools, tree cover was probably markedly lower in the past to promote reproduction and the formation of a large soil seed bank.

Prior to Euro-American settlement, fire, grazing, and other disturbance processes probably slowed forest expansion into rock outcrop ecotones, creating a shifting mosaic of microhabitats in various successional stages (Anderson et al. 1999; Noss 2013; Ware 2002). However, recent changes to historical disturbance regimes, patterns in human land-use, and landscape fragmentation have altered grasslands throughout the southern U.S. (Noss 2013). At present, microhabitat conditions that are optimal for growth and flowering in *A. bibullatus* are now rare in unmanaged LCG ecotones, because fire-intolerant cedar colonizes and persists in all but the thinnest soil microhabitats (Sutter et al. 2011). Cedar encroachment is a homogenizing force that reduces light availability, decreases the abundance of C_4 grasses, increases soil moisture, and favors shade-tolerant bryophytes (Fig. 1; Briggs et al. 2002; Hanberry et al. 2014; Quarterman 1950b). This ‘mesophication’ (Nowacki and Abrams 2008) process in LCG ecosystem mirrors that taking place in woodlands throughout the eastern U.S., where fire-intolerant species are replacing heliophytic forbs and grasses. However, whereas those successional changes

often involve deciduous trees (e.g., maples), in LCGs the dominant woody increaser, cedar, casts year-around shade. The pot study revealed that spring shade (evergreen encroachment) affected *A. bibullatus* growth and biomass more than summer shade (deciduous tree or shrub cover), consistent with the idea that growth characteristics of woody invaders determine the magnitude of their effects in grasslands (Ratajczak et al. 2011b).

4.3 Conservation Implications

Our study in an island-like rock outcrop systems supports a growing body of work in other grasslands and savannas that show woody encroachment poses a threat to the long-term persistence of rare plants. We hypothesize that the decline in demographic performance with woody encroachment in *A. bibullatus* applies to other rare and endemics plants in LCGs, especially legumes (e.g., *Dalea foliosa* and *Trifolium calcaricum*) that are restricted to deeper soil ecotones. If current trends in woody encroachment continue, slow deterministic population declines should be expected, and LCGs could accrue a large extinction debt, as observed in other calcareous grasslands in highly fragmented landscapes (Helm et al. 2006; Saar et al. 2012). Hence, restoration of disturbance regimes in the landscape matrix should be integrated with ongoing efforts to protect remnant outcrops from urban development, reduce threats from human-activities (e.g., off road vehicles), and reintroduce species into protected sites (Albrecht and McCue 2010; Bowen 2011).

In ecotones degraded by woody encroachment, management practices that increase habitat openness and heterogeneity should improve the population viability of

473 rare plants (Possley et al. 2008). For *A. bibullatus*, open, early-successional microhabitats
474 promote growth, flowering, and seed-bank formation, while shadier patches provide
475 opportunities for seedling recruitment. Management efforts should focus primarily on
476 thinning cedar and exotic shrubs, rather than fire-tolerant deciduous trees, to increase
477 light-levels during spring when *A. bibullatus* growth and flowering peaks, while retaining
478 some deciduous canopy shade in summer to improve moisture availability in drought-
479 prone soils. Prescribed burning of the forest matrix surrounding LCGs could help expand
480 suitable habitat in LCG ecotones by reducing cover of fire-intolerant cedar and creating
481 vegetation openings. Fire could improve glade ecotone habitat by increasing light
482 availability, reducing the abundance of dominant species, and enhancing N-limitation,
483 which might provide a competitive advantage for rare legumes (Trammell et al. 2004). In
484 ecotones with high canopy cover and low grass litter, mechanical thinning will be
485 required to modify understory environments before applying fire, since cedars > 2 m tall
486 can survive fires in areas with sparse understory fuel (Briggs et al. 2002).

487 When conserving rare ecotonal plant species adapted to naturally shifting habitat
488 mosaics, reliance on habitat protection strategies alone will be insufficient for their
489 recovery. Conservation and recovery efforts will depend on understanding the spatial and
490 temporal scale in which microhabitat variation influences population dynamics of
491 ecotonal species. Disentangling these effects on different life-history stages may be
492 challenging without conducting experiments and collecting observational data in
493 contrasting microhabitats over multiple years (e.g., Possley et al. 2008). As time since
494 disturbances increases, rare ecotonal plants can persist in suboptimal microhabitats using
495 multiple demographic strategies (e.g., seed bank, emergence in shade, and high adult

survival) (Hylander and Ehrlén 2013). This suggests monitoring schemes that rely on annual counts of aboveground individuals alone will be insufficient to detect population declines following ecotone degradation. However, the ability of tree canopy cover to predict demographic structure in *A. bibullatus* indicates this could be an important parameter to monitor future changes in habitat quality. Our study provides a framework for incorporating successional processes and patch dynamics into the conservation of ecotonal plant species, which could provide insights regarding historical landscape processes (e.g., Fowler et al. 2012; Possley et al. 2008).

Acknowledgements

Funding was provided by the United States Department of Interior (H55901000010, F13AC00106), Tennessee Department of Environment and Conservation -Division of Natural Areas (32701-00385, 32701-0899, 32701-01236), National Science Foundation (DBI-1157030), and the Marcelle Kranzberg Undergraduate Research Scholarship. We thank Andrea Bishop, Geoff Call, David Lincicome, Juan Carlos Penagos, Matt Rhodes, and Gonzalo Rivas for field and logistical assistance. We thank two reviewers for valuable comments on a previous version of the manuscript.

Table 1. Results from the full and reduced RDA (redundancy analysis) model relating demographic structure (numbers of seedlings, vegetation adults, reproductive adults, adult stems, and fruits per plot) to microhabitat variation in *A. bibullatus*. Microhabitat variables that were significant ($P < 0.05$) according to permutation ($n = 999$) ANOVA's are shown in bold.

Variable	Full model (adjusted $R^2 = 0.196$)			Reduced model (adjusted $R^2 = 0.410$)		
	Variance	<i>F</i>	<i>P</i>	Variance	<i>F</i>	<i>P</i>
Habitat	0.818	4.277	0.010	—	—	—
Canopy cover (%)	0.318	1.659	0.208	1.137	8.099	0.001
Grass cover (%)	0.075	0.393	0.804	—	—	—
Forb cover (%)	0.657	3.434	0.040	0.800	5.698	0.002
Moss cover (%)	0.174	0.912	0.448	—	—	—
Litter cover (%)	0.384	2.009	0.132	—	—	—
Rock cover (%)	0.235	1.228	0.357	—	—	—
Bare ground cover (%)	0.442	2.309	0.115	—	—	—
Woody cover (%)	0.059	0.309	0.837	—	—	—
Soil depth (cm)	0.125	0.654	0.590	—	—	—
Soil moisture (%)	0.098	0.512	0.701	—	—	—
Soil CEC (meq/100 g)	0.276	1.445	0.271	0.535	3.808	0.014
Soil NO ₃ (ppm)	0.154	0.806	0.493	—	—	—
Soil Bray P (kg/ha)	0.008	0.039	0.995	—	—	—
Soil pH	0.027	0.144	0.958	—	—	—
Residual	1.148			2.528		

Table 2. Results from model-averaging procedure relating demographic characteristics of *A. bibullatus* to microhabitat variation. Standardized model-averaged regression coefficients (± 1 adjusted SE) are based on averages across all models with $\Delta\text{AIC}_c \leq 2$, weighted by each model's Akaike weight (w_i). Significant regression coefficients ($P < 0.05$) are shown in bold. Microhabitat variables for which there is no data point did not appear in the best models ($\Delta\text{AIC}_c \leq 2$) for that model set (combination of year and demographic variable).

Demographic variable	Year	Canopy cover	Forb cover	Grass cover	Litter cover	Soil depth	Soil N	Soil cec
A) Seedlings								
	2010	-0.03 (0.02)	-0.07 (0.02)	0.06 (0.02)	-0.03 (0.02)	—	-0.07 (0.02)	-0.02 (0.02)
	2011	—	-0.04 (0.01)	—	—	—	NA	NA
	2012	-0.03 (0.03)	-0.19 (0.04)	—	—	-0.07 (0.06)	NA	NA
B) Stem number								
	2010	-0.01 (0.003)	—	—	—	—	-0.005 (0.003)	0.006 (0.003)
	2011	-0.02 (0.006)	—	-0.008 (0.004)	0.01 (0.01) [†]	—	NA	NA
	2012	-0.02 (0.006)	—	—	—	—	NA	NA
C) Reproductive adults								
	2010	-0.44 (0.15)	—	0.26 (0.11)	—	—	0.29 (0.14)	—
	2011	-0.29 (0.07)	—	-0.07 (0.07)	—	—	NA	NA
	2012	-0.51 (0.30) [†]	0.37 (0.24)	—	—	—	NA	NA
D) Legumes								
	2010	-0.07 (0.02)	—	—	—	—	—	0.02 (0.01)
	2011	-0.05 (0.02)	—	-0.007 (0.01)	—	—	NA	NA
	2012	-0.20 (0.11) [†]	0.15 (0.09)	—	—	—	NA	NA

[†] P -values $0.05 \leq P < 0.10$; NA = variable not tested that year

Figure Captions.

Fig. 1. Microhabitat variation in mowed and unmowed LCGs with *A. bibullatus*. A) Scores on the first two principle components axes (PCs, unconstrained PCA) for plots in mowed and unmowed sites. B) Relationships of microhabitat variables relative to PCs. C) Variation in canopy cover among mowed and unmowed sites ($P = 0.037$). D) Biplot from reduced RDA model showing relationship between demographic structure and significant microhabitat variables. Seedlings = Seedling densities; Fruits = Number of fruits; Vegetative = Non-reproductive adult densities; Flowering = Flowering adult stems; Stems = Adult stems per plant; cec=cation exchange capacity.

Fig. 2. Temporal variation (mean $\pm$ 1 SE) in: A) seedling densities, B) average number of stems per adult plant, C) reproductive adult densities, and D) total number of fruits per plot (1 m²) for *A. bibullatus* in mowed and unmowed plots.

Fig. 3. Significant relationships between *A. bibullatus* demographic performance and microhabitat variation based on regression models that best approximated the data. Solid black line represents the fitted line from negative binomial regression models. See Table 2 for significance tests of regression coefficients for each year and demographic variable. Top panels (a-c) represent significant relationships between seedling densities and microhabitat variables. Bottom panels (d-f) represent significant relationships between stem number and fecundity with microhabitat variables.

Fig. 4. Results from demographic survey of *A. bibullatus* in closed, edge, and open habitats pooled over three years (2010-12). A) Relative proportion of demographic stages. B) 1st year seedling survival proportions. C) Per plant number of inflorescences and fruits in reproductive adults. D) Per plant fruit set (proportion of inflorescences with fruit) in reproductive adults. Significant differences ($P < 0.05$) are denoted by the absence of a common letter.

Fig. 5. Results from the pot study where the simulated effects cedar presence (CE⁺) and absence (CE⁻) on *A. bibullatus* seedlings (Sdl) and transplants (Trn) were examined on: A) probability of one-year survival, B) relative growth rates, C) stems per surviving plant, D) shoot mass, E) root mass, and F) root:shoot ratios. Separate tests were conducted for seedlings and transplants. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

References

- Adams, D.A., Walck, J.L., Howard, R.S., Milberg, P., 2012. Forest Composition and Structure on Glade-forming Limestones in Middle Tennessee. *Castanea* 77, 335-347.
- Albrecht, M.A., McCue, K.A., 2010. Changes in demographic processes over long time scales reveal the challenge of restoring an endangered plant. *Restor Ecol* 18, 235-243.
- Albrecht, M.A., Penagos, J.C., 2012. Seed germination ecology of three imperiled plants of rock outcrops in the southeastern United States. *The Journal of the Torrey Botanical Society* 139, 86-95.
- Alofs, K.M., Fowler, N.L., 2012. Loss of native herbaceous species due to woody plant encroachment facilitates the establishment of an invasive grass. *Ecology* 94, 751-760.
- Anderson, R.C., Fralish, J.S., Baskin, J.M. eds., 1999. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK.
- Baskin, J., Baskin, C., Lawless, P., 2007. Calcareous rock outcrop vegetation of eastern North America (exclusive of the Nashville Basin), with particular reference to use of the term “cedar glades”. *The Botanical Review* 73, 303-325.
- Baskin, J.M., Baskin, C.C., 1988. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *J Biogeogr* 15, 829-840.

586 Baskin, J.M., Baskin, C.C., 1989. Cedar glade endemics in Tennessee, and a review of
587 their autecology. *Journal of the Tennessee Academy of Sciences* 64, 63-74.

588 Baskin, J.M., Baskin, C.C., 1999. Cedar glades of the southeastern United States, In
589 Savannas, barrens, and rock outcrop plant communities of North America. eds R.C.
590 Anderson, J.S. Fralish, J.M. Baskin, pp. 206-209. Cambridge University Press, United
591 Kingdom.

592 Baskin, J.M., Baskin, C.C., 2005. Ecology of two geographically restricted *Astragalus*
593 species (Fabaceae), *A. bibullatus* and *A. tennesseensis* of the eastern United States.
594 *Brittonia* 57, 345-353.

595 Bond, W.J., Midgley, G.F., 2000. A proposed CO₂-controlled mechanism of woody plant
596 invasion in grasslands and savannas. *Global Change Biology* 6, 865-869.

597 Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology with R*. Springer New
598 York.

599 Bowen, B., 2011. Natural areas protection at its best: protecting the Tennessee Purple
600 Coneflower (*Echinacea tennesseensis*). *Nat Areas J* 31, 326-330.

601 Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the rate, mechanisms, and
602 consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest.
603 *Ecosystems* 5, 578-586.

604 Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., McCarron,
 605 J.K., 2005. An ecosystem in transition: causes and consequences of the conversion of
 606 mesic grassland to shrubland. *BioScience* 55, 243-254.

607 Brys, R., Jacquemyn, H., Endels, P., De Blust, G., Hermy, M., 2005. Effect of habitat
 608 deterioration on population dynamics and extinction risks in a previously common
 609 perennial. *Conserv Biol* 19, 1633-1643.

610 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a
 611 practical information-theoretic approach, 2nd edn. Springer Science, LLC., New York,
 612 New York.

613 Clarke, G.L., Patterson, W.A., III., 2007. The distribution of disturbance-dependent rare
 614 plants in a coastal Massachusetts sandplain: Implications for conservation and
 615 management. *Biol Conserv* 136, 4-16.

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

619 Colling, G., Matthies, D., Reckinger, C., 2002. Population structure and establishment of
 620 the threatened long-lived perennial *Scorzonera humilis* in relation to environment. *J Appl*
 621 *Ecol* 39, 310-320.

622 Crawley, M.J., 1997. Life history and the environment, In *Plant Ecol.* ed. M.J. Crawley,
 623 pp. 73-131. Blackwell, Oxford, UK.

624 Dawson, W., Fischer, M., van Kleunen, M., 2012. Common and rare plant species
 625 respond differently to fertilisation and competition, whether they are alien or native. *Ecol*
 626 *Lett* 15, 873-880.

627 Doak, D.F., Morris, W., 1999. Detecting population-level consequences of ongoing
 628 environmental change without long-term monitoring. *Ecology* 80, 1537-1551.

629 Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult
 630 plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225-241.

631 Estill, J.C., Cruzan, M.B., 2001. Phytogeography of rare plant species endemic to the
 632 southeastern United States. *Castanea* 66, 3-23.

633 Fowler, N., Center, A., Ramsey, E., 2012. *Streptanthus bracteatus* (Brassicaceae), a rare
 634 annual woodland forb, thrives in less cover: evidence of a vanished habitat? *Plant Ecol*
 635 213, 1511-1523.

636 Gotelli, N.J., Ellison, A.M., 2002. Nitrogen deposition and extinction risk in the northern
 637 pitcher plant, *Sarracenia purpurea*. *Ecology* 83, 2758-2765.

638 Hanberry, B., Kabrick, J., He, H., 2014. Densification and state transition across the
 639 Missouri Ozarks landscape. *Ecosystems* 17, 66-81.

640 Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat
 641 loss and fragmentation. *Ecol Lett* 9, 72-77.

642 Hemmerly, T.E., 1986. Life history strategy of the highly endemic cedar glade species
 643 *Echinacea tennesseensis*. *Castanea* 33, 133-139.

644 Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: Implications for
645 conservation. *Conserv Biol* 6, 324-337.

646 Hylander, K., Ehrlén, J., 2013. The mechanisms causing extinction debts. *Trends Ecol*
647 *Evol* 28, 341-346.

648 Jolls, C.L., Marik, J.E., Hamzé, S.I., Havens, K., 2015. Population viability analysis and
649 the effects of light availability and litter on populations of *Cirsium pitcheri*, a rare,
650 monocarpic perennial of Great Lakes shorelines. *Biol Conserv* 187, 82-90.

651 Jules, E.S., Shahani, P., 2003. A broader ecological context to habitat fragmentation:
652 Why matrix habitat is more important than we thought. *J Veg Sci* 14, 459-464.

653 Kamil, B., 2015. MuMIn: Multi-Model Inference. R package version 1.15.1.

654 Kark, S., 2013. Ecotones and Ecological Gradients, In *Ecological Systems*. ed. R.
655 Leemans, pp. 147-160. Springer New York.

656 Lavergne, S., Garnier, E., Debussche, M., 2003. Do rock endemic and widespread plant
657 species differ under the Leaf-Height-Seed plant ecology strategy scheme? *Ecol Lett* 6,
658 398-404.

659 Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. *For*
660 *Sci* 2, 314-320.

661 Lenth, R.V., Herv, M., 2014. lsmeans: Least-Squares Means. R package version 2.13.

662 Lloyd, K.M., McQueen, A.A.M., Lee, B.J., Wilson, R.C.B., Walker, S., Wilson, J.B.,
 663 2000. Evidence on ecotone concepts from switch, environmental and anthropogenic
 664 ecotones. *J Veg Sci* 11, 903-910.

665 Menges, E.S., Dolan, R.W., 1998. Demographic viability of populations of *Silene regia*
 666 in Midwestern prairies: Relationships with fire management, genetic variation,
 667 geographic location, population size and isolation. *J Ecol* 86, 63-78.

668 Menges, E.S., Quintana-Ascencio, P.F., 2004. Population viability with fire in *Eryngium*
 669 *cuneifolium*: Deciphering a decade of demographic data. *Ecol Monogr* 74, 79-99.

670 Middleton, B.A., 2013. Rediscovering traditional vegetation management in preserves:
 671 Trading experiences between cultures and continents. *Biol Conserv* 158, 271-279.

672 Morris, A.B., Baucom, R.S., Cruzan, M.B., 2002. Stratified analysis of the soil seed bank
 673 in the cedar glade endemic *Astragalus bibullatus*: evidence for historical changes in
 674 genetic structure. *Am J Bot* 89, 29-36.

675 NOAA, 2013. State of the Climate: Drought for Annual 2012. National Centers for
 676 Environmental Information, <http://www.ncdc.noaa.gov/sotc/drought/201213>.

677 Noss, R.F., 2013. *Forgotten Grasslands of the South*. Island Press, Washington DC.

678 Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. *Endangered ecosystems of the United States:*
 679 *a preliminary assessment of loss and degradation*, p. 59, Washington D.C.

680 Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and mesophication of forests in
 681 the eastern United States. *BioScience* 58, 123-138.

682 Odum, E.P., 1983. Basic ecology. Saunders College Publishing, Philadelphia.

683 Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara,
684 R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. vegan:
685 Community Ecology Package, R package version 2.3-0.

686 Pardini, E.A., Vickstrom, K.E., Knight, T.M., 2015. Early successional microhabitats
687 allow the persistence of endangered plants in coastal sand dunes. PLoS ONE 10,
688 e0119567.

689 Pavlovlic, N.B., 1994. Disturbance-dependent persistence of rare plants: anthropogenic
690 impacts and restoration implications, In Restoration of Endangered Species: Conceptual
691 Issues, Planning and Implementation. eds M.L. Bowles, C.J. Whelan, pp. 159-193.
692 Cambridge University Press, New York.

693 Possley, J., Maschinski, J., Rodriguez, C., Dozier, J.G., 2008. Alternatives for
694 reintroducing a rare ecotone species: Manually thinned forest edge versus restored habitat
695 remnant. Restor Ecol 17, 668-677.

696 Quarterman, E., 1950a. Ecology of cedar glades. I. Distribution of glade flora in
697 Tennessee. Bull Torrey Bot Club 77, 1-9.

698 Quarterman, E., 1950b. Major plant communities of Tennessee cedar glades. Ecology 31,
699 234-254.

700 Quintana-Ascencio, P.F., Weekley, C.W., Menges, E.S., 2007. Comparative demography
701 of a rare species in Florida scrub and road habitats. Biol Conserv 137, 263-270.

702 R Core Team, 2015. R: A language and environment for statistical computing. R
703 Foundation for Statistical Computing, Vienna, Austria.

704 Ratajczak, Z., Nippert, J.B., Briggs, J.M., Blair, J.M., 2014. Fire dynamics distinguish
705 grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains
706 of North America. *J Ecol* 102, 1374-1385.

707 Ratajczak, Z., Nippert, J.B., Collins, S.L., 2011a. Woody encroachment decreases
708 diversity across North American grasslands and savannas. *Ecology* 93, 697-703.

709 Ratajczak, Z., Nippert, J.B., Hartman, J.C., Ocheltree, T.W., 2011b. Positive feedbacks
710 amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere* 2, art121.

711 Risser, P.G., 1995. The status of the science examining ecotones. *BioScience* 45, 318-
712 325.

713 Saar, L., Takkis, K., Pärtel, M., Helm, A., 2012. Which plant traits predict species loss in
714 calcareous grasslands with extinction debt? *Divers Distrib* 18, 808-817.

715 Schielzeth, H., 2010. Simple means to improve the interpretability of regression
716 coefficients. *Methods in Ecology and Evolution* 1, 103-113.

717 Schleuning, M., Matthies, D., 2009. Habitat change and plant demography: Assessing the
718 extinction risk of a formerly common grassland perennial. *Conserv Biol* 23, 174-183.

719 Skogen, K.A., Holsinger, K.E., Cardon, Z.G., 2011. Nitrogen deposition, competition and
720 the decline of a regionally threatened legume, *Desmodium cuspidatum*. *Oecologia* 165,
721 261-269.

722 Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas,
 723 D.G., Pennings, S., 2005. Functional- and abundance-based mechanisms explain diversity
 724 loss due to N fertilization. *Proc Natl Acad Sci U S A* 102, 4387-4392.

725 Sutter, R.D., Govus, T.E., Smyth, R.L., Nordman, C., Pyne, M., Hogan, T., 2011.
 726 Monitoring change in a Central U.S. calcareous glade: resampling transects established in
 727 1993. *Nat Areas J* 31, 163-172.

728 Thompson, J.N., Walck, J.L., Hidayati, S.N., 2006. Microhabitat requirements of the
 729 federally endangered *Dalea foliosa*, with recommendations on establishment of new
 730 populations. *Castanea* 71, 94-104.

731 Trammell, T.L.E., Rhoades, C.C., Bukaveckas, P.A., 2004. Effects of prescribed fire on
 732 nutrient pools and losses from glades occurring within oak-hickory forests of central
 733 Kentucky. *Restor Ecol* 12, 597-604.

734 USFWS, 2011. Recovery Plan for *Astragalus bibullatus* (Pyne's Ground-plum). p. 43,
 735 Atlanta, Georgia.

736 Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. *Annu*
 737 *Rev Ecol Syst* 31, 197-215.

738 Vitt, P., Havens, K., Kendall, B.E., Knight, T.M., 2009. Effects of community-level
 739 grassland management on the non-target rare annual *Agalinis auriculata*. *Biol Conserv*
 740 142, 798-805.

741 Ware, S., 2002. Rock outcrop plant communities (Glades) in the Ozarks: A synthesis.
742 The Southwestern Naturalist 47, 585-597.

743 Williams, N.S.G., Morgan, J.W., McCarthy, M.A., McDonnell, M.J., 2006. Local
744 extinction of grassland plants: the landscape matrix is more important than patch
745 attributes. Ecology 87, 3000-3006.

746 Wood, S., Scheipl, F., 2014. gamm4: Generalized additive mixed models using mgcv and
747 lme4. R package version 0.2-3.

748

Figure

2-column fitting image

Figure

2-column fitting image

Figure

2-column fitting image

Figure

2-column fitting image

Figure

2-column fitting image