Implications of Food Web Interactions for Restoration of Missouri Ozark Glade Habitats

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Abstract

Ozark glades are gaps in forested areas that are dominated by grasses and forbs growing in rocky, nutrient-poor soil. Historically, these open, patchy habitats were maintained by natural and anthropogenic fire cycles that prohibited tree encroachment. However, because of decades of fire suppression, glades have become overgrown by fire-intolerant species such as Eastern red cedar (*Juniperus virginiana*). Current restoration practices include cutting down invasive cedars and burning brush piles, which represent habitat for Northern fence lizards (*Sceloporus undulatus*). Because *Sceloporus* actively consumes herbivores, we hypothesized that the presence of these lizards in and around brush piles might result in a trophic cascade, whereby damage on native plants is reduced. Field surveys across six Missouri glades indicated that lizard activity was minimal beyond 1 m from habitat structures. This activity pattern reduced grasshopper abundance by 75% and plant damage by over 66% on *Echinacea paradoxa* and *Rudbeckia missouriensis* near structures with lizards. A field transplant experiment demonstrated similar reductions in grasshopper abundance and damage on two other glade endemic species, *Aster oblongifolius* and *Schizachyrium scoparium*. These results demonstrate that future glade restoration efforts might benefit from considering top-down effects of predators in facilitating native plant establishment.

Key words: biomanipulation, *Sceloporus undulatus*, trophic cascade.

Introduction

Restoration efforts commonly focus on manipulations and reinstatement of the bottom trophic level—plants. However, consumers of plants (herbivores), and consumers of those consumers (carnivores), can often have profound effects on the growth rates, population dynamics, biodiversity, and ecosystem functioning of plant communities (reviewed in Huntly 1991). Although the importance of such food web effects is still debated, particularly in terrestrial ecosystems (Strong 1992; Leibold et al. 1997; Chase 2000; Chase et al. 2000; Polis et al. 2000; Schmitz et al. 2000; Shurin et al. 2002), it is apparent that an effective restoration strategy needs to consider the entire community, including the effects of consumers in food webs (Bevill et al. 1999; Howe et al. 2002; Ruhren & Handel 2003). Indeed, the recognition of the importance of consumers has already influenced restoration efforts in some aquatic and terrestrial agricultural ecosystems. In aquatic communities the addition of piscivorous (fish eating) fish causes a decline in the abundance of zooplanktivorous fish, thus resulting in more grazers and less algae (Bergman et al. 1999; Lathrop et al. 2002). Similar recommendations have been made for riparian plant management with introduced wolves filling the role of plant mutualists (Ripple & Beschta 2003). In other terrestrial systems, attempts at the biocontrol of crop pests have centered on increasing physical structure with the addition of mulch to augment habitat for predators such as spiders (Riechert & Bishop 1990; Brust 1994; Symondson et al. 2002).

In this study we examined the indirect effects of native insectivorous lizards (*Sceloporus undulatus*) on the herbaceous plant communities in actively restored Missouri (U.S.A.) Ozark glades through their direct effects on herbivorous insects. Glades are rocky outcrops contained within forested areas where poor abiotic conditions such as low soil moisture and acidic, nutrient-poor soils limit plant productivity (Nelson 1987; Baskin & Baskin 2000). These outcrops are the result of years of landform erosion, which allows the bedrock to break the surface of the glade's thin soil. Glades resemble prairie communities of the western United States and share many plant and animal genera with those systems (Nelson & Ladd 1980). In addition, many glade plant species are relictual and endemic, and glade species are often typical of hotter and drier conditions of desert areas (Baskin et al. 1995; Baskin & Baskin 2000; McClain & Ebinger 2002). Historically, glades were maintained as herbaceous (grass and forb) communities in part by a regular fire cycle that excluded fire-sensitive species, including most trees (Templeton et al. 2001; Ware 2002). Fire suppression following European settlement has allowed native fire-sensitive trees to invade many of these glade habitats (Bergmann & Chaplin 1992; Baskin & Baskin 2000; Ware 2002). Of particular

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concern is the Eastern red cedar (*Juniperus virginiana*), because it further fragments glade habitats and forms dense stands that shade out glade endemic plants.

Recently, Ozark glades have been targeted by restoration efforts. Restoration of glades typically requires several seasons of prescribed burns and physical removal of cedar trees and saplings, combined with hand planting of glade endemics (Davis 1982). Often, because of high seedling mortality and low germination success, transplantation of juvenile plants is the most effective way of reestablishing glade species (J. C. Walker 2003, Tyson Research Center, personal communication; Ruhren & Handel 2003). However, even juvenile plants that have been planted may not become successfully established if they are sufficiently consumed by grasshoppers (Orthoptera: Acrididae) and other herbivorous insects. In Missouri Ozark glades, leaf-chewing herbivores can cause substantial damage (approximately 10–80%) to a wide variety of glade plants. For example, insect herbivory on the glade perennial *Liatris cylindracea* has been shown to reduce fecundity by as much as 83% and establishment of seedlings in the next season by over 50% (Kelly & Dyer 2002). Because grasshoppers and larval lepidopterans are the most abundant groups of herbivorous insects (in terms of biomass; $\geq$80%) in glades (Chase, unpublished data; Kelly & Dyer 2002), minimizing their impact can substantially reduce herbivore damage in these communities.

We hypothesize that the restoration of Ozark glades will be enhanced by explicitly considering the predators and their concomitant food web interactions. That is, predators of insects can reduce herbivore density in glade ecosystems, thereby reducing losses of plants to abundant grasshoppers and other chewing herbivores. One predator of grasshoppers that can be quite common in Ozark glades is the Northern fence lizard *S. undulatus* (hereafter, *Sceloporus*). *Sceloporus* is usually restricted in its foraging to areas on and around cover objects, such as downed logs, brush piles, and rock piles (Angert et al. 2002; James & M'Closkey 2002). We focus on grasshopper abundance, because in Missouri, grasshoppers constitute a majority of the summer and fall diet of *Sceloporus* (Marion 1970), with larval lepidopterans constituting a small fraction of the diet (DeMarco et al. 1985). Also, observations and experiments in California meadows showed that Western fence lizards (*S. occidentalis*) decreased grasshopper abundance and subsequent damage on plants (Chase 1998), although this effect was most pronounced within 10 m of cover objects.

We suspected that a trophic cascade (i.e., an indirect positive effect of predators on plants through their negative effects on herbivores) due to *Sceloporus* feeding in glade habitats might decrease herbivory on target plants, thus potentially increasing the transplant success of glade endemics and facilitating glade restoration efforts. We further predicted that herbivory would be reduced on plants that occurred near structures supporting lizards, relative to plants that were not near lizard-occupied structures. We tested this hypothesis through surveys of lizard activity, grasshopper abundance, and plant damage in natural glades, along with an experiment in which we planted glade plants at three different distances from cover objects to simulate common restoration practices in a glade that is currently undergoing restoration. Our results indicate a potential role for predation in facilitating glade restoration efforts. This is particularly pertinent, because current glade restoration projects often remove brush piles and other potential cover habitats. We conclude that future restoration efforts would benefit by providing cover habitats for lizards, which could facilitate plant establishment.

Methods

Glade Sampling

To assess the natural patterns in herbivory which might be attributed to trophic cascades, we measured *Sceloporus* activity, grasshopper density, and levels of herbivory on three plant species in six recently restored glades in southeastern Missouri. We collected data at two glades at Washington University's Tyson Research Center (St. Louis County) and four glades at Meramec State Park (Franklin County). These glades are of similar size and consist of comparable plant communities occurring in thin, nutrient-poor soil over dolomitic limestone bedrock (Walker 1998; Baskin & Baskin 2000; Ware 2002). Restoration efforts have recently (within the last 10–15 years) been initiated on all our study glades and consist of intensive management involving physical removal of Eastern red cedar trees, prescribed burns, and reseeding of native glade-specific plants.

To characterize lizard foraging patterns, we estimated *Sceloporus* activity weekly by repeatedly observing lizards between 0800 and 1800 hr over a 10-week period in the two glades at Tyson, and during a 1-day sampling transect through the four Meramec glades. We estimated activity by having one observer walk transects throughout each glade, noting the presence and activity of all *Sceloporus*, and measuring the distance to the nearest cover object (e.g., downed logs, brush piles, bushes). The repeated observations of lizard behavior at Tyson were made on the same lizard populations, and therefore are not independent. However, because the same patterns of activity were observed for the Meramec population, all data for lizard activity are presented as a single dataset.

We estimated grasshopper densities and amount of plant damage caused by chewing herbivores at three distances from cover objects used by lizards. For grasshoppers, we haphazardly chose five plots (0.1 m^2) at each of the three distances ($\leq$1, 8, and 16 m) and disturbed the 0.1-m^2 area with a stick, counting all grasshoppers that moved from the plot. This is an established and quick method of estimating grasshopper abundance (Onsager & Henry 1977). Subsequently, we estimated the relative amount of leaf tissue missing due to chewing herbivores for three different glade endemics: a sedge (*Carex* sp.) and two forbs (*Echinacea paradoxa* and *Rudbeckia missouriensis*). In each glade we haphazardly chose three plants from each species at each distance and estimated the relative amount of leaf tissue consumed by chewing herbivores. Estimates were made visually and rounded to the nearest 10% following established methods (Van Zandt & Agrawal 2004). These plants were sampled from the same cover objects used for the grasshopper estimates. We were interested in general patterns across glades; therefore, we averaged each of the three samples at each distance and analyzed glades as replicates. Samples of herbivore density and plant damage were taken at the end of the growing season (August 2003), so the effects of differential herbivory would have been apparent at the time of censusing.

Transplant Experiment

To test the effects of the presence of *Sceloporus* on herbivore impacts on transplanted plants, we planted seedlings of three species common to glades in Missouri: an herb (*Aster oblongifolius*), a legume (*Dalea purpurea*), and a grass (*Schizachyrium scoparium*). Seedlings were obtained from Missouri Wildflowers Nursery (http://www.mowildflowers.net) and were size matched before transplanting. In June 2003 we transplanted plants into the Southwest glade at Tyson Research Center. Plants were transplanted in groups at three different distances from the nearest brush pile with at least one *Sceloporus* occupant: near (<1 m), middle (8 m), and far (16 m). At each distance, five groups of plants were established, with each group consisting of one replicate plant from each species. Plants were initially watered to facilitate establishment, but after the second week no supplemental water was added. At the end of the summer (August 2003), we took damage measurements by recording the percentage of each leaf that had been eaten, as above. We also monitored grasshopper abundance near these piles during a one-time survey.

Statistical Analysis

We assessed the effects of distance from lizard-occupied structures on grasshopper density and plant damage with separate analyses of variance using SYSTAT (Wilkinson 1998). Grasshopper density data were log transformed, and percent damage values were arcsine square root transformed to meet the assumptions of parametric statistics; however, untransformed means and standard errors are reported in the figures.

Results

Glade Sampling

In field surveys *Sceloporus* activity was usually near cover objects (Fig. 1), such as brush piles, downed logs, and small shrubs. Over 85% of all lizard observations were of individuals within 1 m of cover objects. In contrast, grasshopper densities increased significantly at greater distances from cover objects (Fig. 2; $F_{[2,9]} = 21.1$, $p < 0.0001$). In censuses conducted at 16 m from cover objects, grasshoppers were over four times more abundant than in censuses at 1 m. Finally, plant damage by chewing herbivores increased substantially with distance from cover for two of the three plant species surveyed at the Meramec glades (Fig. 3; *Rudbeckia* $F_{[2,9]} = 6.5$, $p = 0.018$; *Echinacea* $F_{[2,9]} = 8.18$, $p = 0.009$). Damage on *Rudbeckia* and *Echinacea* was over three times higher at plants over 8 m away from cover objects than on plants within 1 m of cover objects.

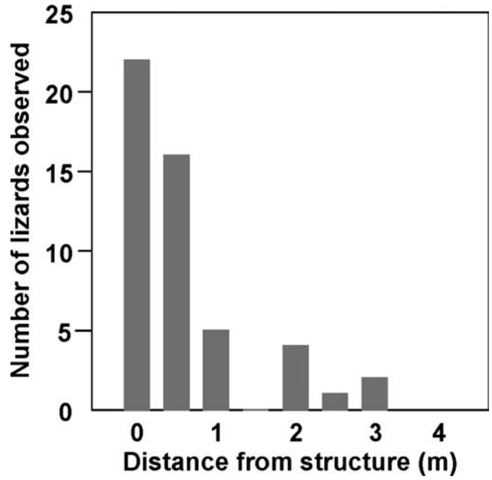

Figure 1. Lizard activity with distance from habitat structures. Data are total counts of lizard observations from all six glades described in the Methods and represent multiple observations of individual lizards at different distances from cover objects.

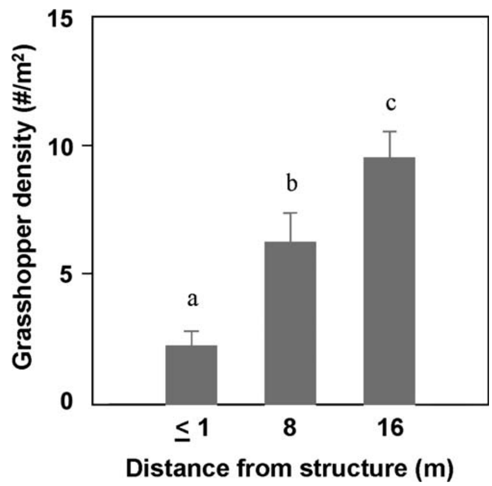

Figure 2. Grasshopper density increases with distance from structure across four glades at Meramec State Park. For each glade, grasshopper density was sampled in five 0.1-m^2 quadrats at three distances from cover objects used by *Sceloporus* lizards: near (≤1 m), middle (8 m), and far (16 m). Bars with the same letter are not different in Tukey adjusted post hoc comparisons.

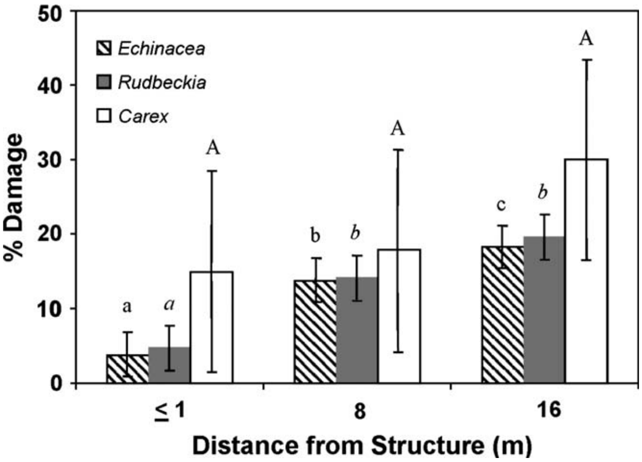

Figure 3. Plant damage increases with distance from structure across four glades at Meramec State Park. For each glade and distance from cover object, plant damage was estimated on three randomly selected plants. Data were collected from the same cover objects as in Figure 2. Bars with the same letter are not different in Tukey adjusted post hoc comparisons between treatments for each species.

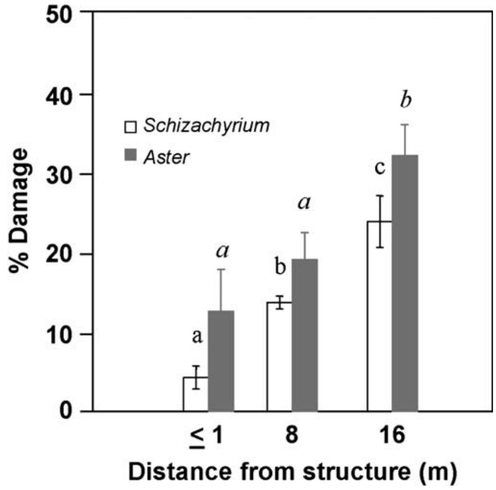

Figure 4. Plant damage increases with distance from structure in transplanted plants at the Tyson experimental glade. Plants were established in groups at three different distances from the nearest brush pile: near (<1 m), middle (8 m), and far (16 m). Bars with the same letter are not different in Tukey adjusted post hoc comparisons between treatments for each species.

Plant damage did not change significantly with distance for the sedge ($F_{[2,9]} = 0.39, p = 0.69$) (Fig. 3).

Transplant Experiment

In the Southwest glade at Tyson, a one-time estimate indicated a reduction of grasshopper density with proximity to structures, similar to results from the Meramec glades. The estimate of grasshopper density at 16 m (9/m^2) was over 3.5 times higher than that at the 1- and 8-m distances (both = 2.5/m^2).

Following initial transplantation, the clover experienced high mortality (>50%), which was apparently due to transplant shock, because most plants were withered rather than consumed by herbivores. For this reason, we were not able to obtain estimates of herbivory for this species. Neither *Aster* nor *Schizachyrium* experienced any transplant mortality. For both these species, the amount of damage by chewing herbivores increased with distance from cover objects (Fig. 4). Compared to plants near structures, plant damage at 16 m was almost three times higher on *Aster* and over five times higher on *Schizachyrium*.

Discussion

Our results suggest that the presence of lizards reduced grasshopper abundance as well as levels of herbivory, consistent with trophic cascades found in other terrestrial systems (e.g., Chase 1998; Moran & Hurd 1998). However, the impact of *Sceloporus* in Missouri glades appears to be limited by the availability of suitable cover objects (e.g., brush and rock piles), because their effects were limited to distances close to those objects. Thus, although a trophic cascade was evident from lizards to plants, the overall importance of this cascade to the entire community depends on the amount of cover available to the lizards. Chase (1998) found similar effects of cover on the impacts of the Western fence lizard in California. These structures are used by lizards as refuges from predators (e.g., birds and snakes), perches for hunting and defending territories, and for thermoregulation (Chase 1998; Angert et al. 2002). We used pooled densities of all grasshopper species in the analysis. However, because different grasshopper species have different host plant preferences (Bernays & Chapman 1994), it is possible that lizards differentially altered the density of different species of grasshoppers, which could confound our results. Nevertheless, we did not note any compositional differences among grasshoppers relative to distance from structures, and our results appear to be robust to this level of grouping in these glades.

In our field survey, proximity to structures occupied by *Sceloporus* decreased herbivore damage to two of the three surveyed plant species, *Rudbeckia* and *Echinacea*. Although these results suggest that consumption of chewing herbivores by lizards was responsible for this trophic cascade, we cannot rule out the possibility that grasshoppers and other insects avoided brush piles and downed logs because they alter microclimate factors such as temperature. However, Chase (1998) found that the density of grasshoppers in California meadows was not affected by the proximity to stumps, logs, or brush piles that were unoccupied by lizards. Therefore, we assume that the presence of *Sceloporus* is largely responsible for decreasing herbivore density and plant damage near structures in these glade habitats.

Our results showed a slight trend for decreasing damage on the sedge with increasing proximity to lizard structures, although the distance effect was not significant. Chase

(1998) found that the proportion of forb cover decreased with distance from structures with lizards, indicating that the grasshoppers in that study preferentially consumed forbs and avoided grasses and sedges. This preferential consumption by insect herbivores is common in grasslands and has the potential for altering plant community composition (Ritchie et al. 1998). Such a preference by herbivorous insects could explain why *Sceloporus* were not as effective in decreasing herbivory on the sedge as they were with the herbs. Indeed, the most common species of grasshoppers at our sites were members of the *Melanoplus* genus; these species are known to include a low proportion of grasses and sedges into their diet (Joern 1983). However, this would not explain the fact that we did find significant distance effects for the grass, *Schizachyrium*, in the transplant experiment. An alternative explanation for the lack of a result for the sedge (*Carex*) would be that *Sceloporus* did not readily consume the herbivores that feed on sedges, such as larval lepidopterans.

Our results for *Sceloporus* activity seem slightly inconsistent with the responses of either grasshopper density or estimated levels of herbivory, because most observations of lizards were limited to less than 1 m of cover objects, yet their effects were apparently detectable at distances of 8 m. However, this apparent inconsistency relies on our observations of lizards being an accurate representation of their home ranges. For our lizard observations, we recorded 50 sightings of approximately 10–20 different individuals, far less than the minimum of 10 observations per individual required to accurately assess home-range size for this species (Haenel et al. 2003). Therefore, our data on *Sceloporus* activity near cover objects are more indicative of their behavior as central-place foragers (Chase 1998) rather than an accurate representation of their home-range sizes.

Because we found that lizard foraging was highest in areas adjacent to brush piles and downed logs, the spatial arrangement and availability of cover objects plays an important role in the direct effects of lizards on herbivorous insects and their indirect effects on plants. This provides an obvious and direct implication for restoration efforts. Specifically, we suggest that restoration efforts in these glade ecosystems be broadened to consider not only plants but also the interactions of plants with the rest of the food web. If damage by insects, particularly large mobile insects such as grasshoppers, has a strong negative influence on the restoration of plant communities, this influence can be reduced by facilitating the foraging activities of lizards. Such facilitation could include increasing the number of available cover objects and making sure that these structures are evenly spaced throughout glade habitats. Currently, it is common practice when restoring glade habitats to cut down all the trees within an overgrown glade and systematically remove and burn all the wood (P. Van Zandt 2003, Washington University in St. Louis, personal observation). One recommendation for future restoration efforts that takes a food web perspective into account involves leaving some of these brush piles, downed logs, or other structures which can serve as lizard refugia, thus facilitating plant growth and establishment by reducing plant losses to herbivores. Incorporation of these structures in restored glade and prairie systems provides the additional benefit of generating spatial heterogeneity naturally present in these communities (Cottam 1987; Ware 2002) by providing refuges to plant species otherwise attractive to insects.

The practice of managing the abundance of unwanted plants (especially phytoplankton) by manipulating top trophic levels in the food web is a commonly employed technique in the restoration of lakes (known as biomanipulation, e.g., Bergman et al. 1999; Lathrop et al. 2002). Although somewhat controversial (Strong 1992; Chase 2000; Polis et al. 2000), evidence for the importance of trophic cascades and food web interactions for terrestrial ecosystems is growing (Schmitz et al. 2000; Halaj & Wise 2001; Shurin et al. 2002). The effects of habitat structure on terrestrial herbivore abundance and plant damage have been investigated in both natural and agricultural systems (Riechert & Bishop 1990; Brust 1994; Symondson et al. 2002). For example, spiders have a greater impact on reducing the numbers of phloem-feeding planthoppers in more structurally complex stands of *Spartina alterniflora* (Denno et al. 2002). Similarly, spiders strongly reduced herbivore consumption of soybean plants within 1 m of spider habitat refugia (Halaj et al. 2000). Therefore, we suggest that using higher trophic levels (i.e., predators) for the purpose of biomanipulation in glade communities may be an effective practice for facilitating plant establishment and community restoration through a reduction in herbivore pressure.

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