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Biological soil crust cover is negatively related to vascular plant richness in Ozark sandstone glades[1]

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Abstract. Sandstone glades in the Ozark highlands contain unique communities of vascular plants, including several species of conservation concern, as well as abundant communities of terricolous cryptogams—collectively termed *biological soil crusts*. Biological soil crusts have important ecological roles in grassland systems, such as preventing erosion and retaining soil moisture. Despite the conservation importance of sandstone glades, this ecosystem has received little scientific attention, and the drivers of plant diversity and soil crust prevalence in sandstone glades are poorly understood. In this study, we assessed relationships between soil crust cover and vascular plant species richness and tested whether dominance shifts from soil crusts to vascular plants along a soil gradient. Soil crust cover was negatively related to vascular plant species richness, and vascular plant richness increased (and crust cover decreased) with increasing soil organic matter. As soil organic matter increased, the proportion of perennial vascular plants in the community also increased. These results provide some of the first quantitative evidence for drivers of plant diversity patterns in Ozark sandstone glades and suggest that soil characteristics have an important role in structuring the distributions of plants and crusts in sandstone glades.

Key words: biological soil crusts, edaphic communities, lichens, outcrop communities, plant diversity

Sandstone glades are rocky, acidic grasslands that occur in the wooded Ozark highlands in Missouri and Arkansas, as well as in neighboring regions (Nelson and Ladd 1983, Heikens and Robertson 1995). Sandstone glades are usually spatially discrete and range in size from < 1 to 9 ha, often occurring in complexes (Nelson 2014). They have shallow, poorly developed soils that are interspersed with areas of exposed sandstone bedrock (Heikens 1999). These glades are characterized by unique vascular plant and cryptogam (lichen and moss) communities that are adapted to the harsh, seasonally xeric soil environment (Ladd and Nelson 1982). Several plant species of conservation concern occur in sandstone glades, including the federally listed *Geocarpon minimum* Mack. The recent mapping of hundreds of hectares of sandstone glades that were previously little known to ecologists in southwestern Missouri highlights that these communities have been rarely studied (Nelson 2014). Sandstone glade plant communities have been described from a natural history perspective (Nelson and Ladd 1983, Heikens 1999, Nelson 2005), and community patterns have been studied at individual localities (D. Jeffries 1985, Jeffries 1987), but there has been little quantitative analysis of vascular plant and cryptogam communities in Ozark sandstone glades at a regional scale.

Sandstone glades are ecologically similar to igneous glades, which also occur in the Ozark region; both have sandy, acidic soils, and share numerous dominant plant species (Ladd and Nelson 1982, Nelson 2005). Sandstone glades also bear some resemblance to the flat-rock limestone cedar glades of the southeastern USA; both glade types have distinctive, diminutive plant communities that occur in thin soils among patches of exposed bedrock (Quarterman 1950, Baskin and Baskin 2000, Baskin *et al*. 2007). Dolomite glades—the most abundant glade type in the Ozark region—are less similar to sandstone glades, and share relatively few species. Dolomite glades

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tend be more productive, densely vegetated habitats that bear a stronger resemblance to tallgrass prairies than they do to the sparse plant communities in sandstone glades (Nelson 2005).

Ecologists in the mid-1900s described glades of various substrates as early successional communities in a seral trajectory toward woodlands (Steyermark 1940, Quarterman 1950). More recently, and concurrent with the development of the old-growth grasslands concept (Veldman *et al*. 2015), relic glades have been recognized as late-successional communities that have been maintained in otherwise-wooded landscapes through a combination of topoedaphic factors and frequent, low-intensity fires (Nelson 2005, Ware 2002). Although anthropogenic disturbance, such as grazing domestic cattle, was historically seen as favorable to maintaining open glade structure and associated herb communities (Quarterman 1950), glades are now more commonly viewed as sensitive habitats that require judicious stewardship (Nelson 2005). Many Ozark ecosystems, including glades, are now managed with prescribed fire to emulate historical fire regimes and to slow the encroachment of woody vegetation, which, if unchecked, can eventually lead to habitat conversion (Nelson 2005). Areas of glades with particularly shallow, low-nutrient soils—such as harsh sandstone glades—may be more resistant to encroachment even with little or no fire (Heikens 1999). However, fire is no doubt needed to maintain the historic composition and structure of deeper soil areas of glades and to maintain a habit structure in the surrounding matrix communities, which promotes functional connectivity among glades (Templeton *et al*. 2001, Albrecht *et al*. 2015). Recent research from limestone cedar glades in the southeastern USA suggests that extensive prairie and savanna-like communities, dominated by warm-season grasses, once occurred in areas with deeper soils surrounding glades, which are now occupied by dense thickets of cedar (*Juniperus*) and broadleaf shrubs (Albrecht *et al*. 2015). This raises the question of whether more-extensive grasslands have historically occupied some of the deeper soil areas surrounding sandstone glades that are now wooded as well.

Terricolous (soil-dwelling), cryptogam-dominated soil crusts are a conspicuous component of sandstone glade communities, forming extensive mats in the shallowest soil zones. Lichens often dominate these soil crust communities, with extensive patches of fruticose lichens (*Cladonia* P. Browne *spp*., especially *C. caroliniana* Tuck.) and smaller patches of foliose lichens forming on thin soils over rock. Terricolous mosses can also be abundant in sandstone glades, and free-living cyanobacteria and algae are often present in crust communities. Soil crust cryptogams have important ecological roles; they prevent wind and water erosion by anchoring the soils, and they alter hydrologic dynamics by slowing both percolation of water into the soil and evaporation of water out of the soil (Belnap *et al*. 2001). In addition, soil crust cryptogams often have important roles in nutrient cycling and can be significant sources of nitrogen for vascular plants (Belnap 2001).

Soil crust cover can influence plant diversity patterns at a local scale. There is evidence that soil crusts can both promote and inhibit seed germination and plant establishment in different contexts (Belnap *et al*. 2001). Soil crusts can be associated with endemic vascular plants (Meyer 1986) and may prevent invasion by exotic species (Deines *et al*. 2007). However, soil crusts, when abundant, can also exclude native vascular plants, with effects varying by crust morphological group and species (Sedia and Ehrenfeld 2003, Soudzilovskaia *et al*. 2011). Plant guilds, such as perennial and annual species, may also respond differently to crusts (Langhans *et al*. 2010). The relative importance of environmental gradients and local interactions for plant and soil crust communities remains incompletely understood (Briggs and Morgan 2008).

Soil characteristics have been shown to be associated with fine-scale plant-community variation in Ozark sandstone glades, suggesting that soil may also structure larger-scale diversity patterns in this system, such as species turnover among glades (D. L. Jeffries 1985, Jeffries 1987). Evidence from similar systems also indicates that variation in soil has a substantial influence on plant communities. For example, several descriptive studies of limestone cedar glades in the central basin of Tennessee have emphasized responses of vascular plant and cryptogam communities to fine-scale variations in soil depth and the arrangement of underlying bedrock formations (*e.g*., Quarterman 1950; reviewed by Baskin *et al*. 2007). Recent research has shown that soil resource availability is a strong driver of vascular plant species richness in dolomite glades, another rock-outcrop community that is widespread in the Ozarks (Miller *et al*.

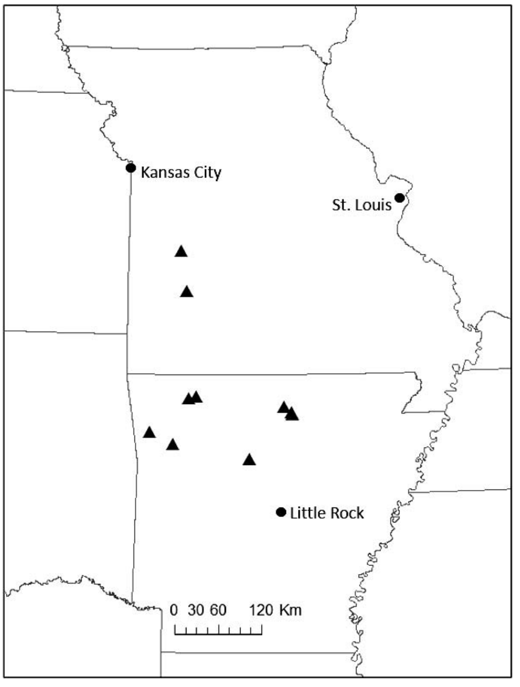

Fig. 1. Map of ten study site locations (indicated by triangles) in Arkansas and Missouri. Site names and locations are listed in Table 1.

2015). Soil crusts have also been shown to respond to soil characteristics in other systems (Thompson *et al.* 2006, Root and McCune 2012).

We explored whether soil characteristics influence vascular plant species richness and cryptogam cover in sandstone glades. We examined evidence for whether dominance shifts from cryptogams to vascular plants as soil resource availability increases. We analyzed whether annual plants make up a greater proportion of the vascular plant community at sites with lower-resource soils. Finally, we examined whether vascular plant richness and crust cover have an inverse relationship, which could occur because each group is favored by different environmental conditions and because of negative interactions between vascular plants and crust species.

Methods. Community Sampling. To test relationships among plant species richness, soil crust cover, and soil resource availability, we sampled communities in 10 sandstone glades across the Ozarks and in areas of the adjacent Osage Plains (hereafter *Ozarks*) in Missouri and Arkansas (Fig. 1; Table 1). Study sites were chosen through consultation with land managers, avoiding sampling glades that land managers indicated had been damaged by past land use practices, such as intensive grazing. Because some sandstone glades that managers consider to be high-quality, reference-condition sites are managed with prescribed fire, whereas others are not, we did not restrict site selection based on fire history.

To quantify plant richness and lichen cover, we established one 100-m^2 (2 m $\times$ 50 m) vegetation plot at each study site. Within each glade, study plots were randomly located within open areas (*i.e.*, with $<$ 10% woody vegetation cover) to avoid confounding effects of shading. All vascular plants within each plot were identified to species. Vascular plant taxonomy follows Yatskievych

Table 1. List of study sites, locations, and ownerships. ADPT = Arkansas Department of Parks and Tourism; AGFC = Arkansas Fish and Game Commission; ANCH = Arkansas Natural Heritage Commission; MDC = Missouri Department of Conservation; USACE = US Army Corps of Engineers, USFS = US Forest Service.

Site	State	County	Ownership	Latitude	Longitude	Organic matter (%)	Topographic slope (°)	Vascular plant richness	Average soil crust cover
Bona Glade	MO	Dade	USACE	37.5467	−93.6919	1.9	1	22	86
City Rock	AR	Stone	USFS	36.1000	−92.1782	2.5	2	16	61
Devil's Den	AR	Washington	ADPT	35.7831	−94.2487	3.7	18	35	0
Devil's Knob	AR	Izard	ANHC	36.0028	−92.0500	1.4	0	24	34
Holbrook Glade	AR	Conway	USFS	35.4466	−92.7200	5.8	2	29	10
Jellico Hollow	AR	Madison	AGFC	36.2029	−93.6583	3.6	1	35	45
Lichen Glade	MO	St. Clair	MDC	38.0542	−93.7926	4.2	7	37	18
Ninestone Glade	AR	Carroll	Private	36.2342	−93.5463	4.3	7	35	26
Optimus Glade	AR	Stone	USFS	36.0309	−92.0748	1.4	2	26	53
Rossen Hollow	MO	Franklin	USFS	35.6312	−93.8892	6.3	10	33	6
Mean						3.5	5	29	34
SD						1.7	6	7	27

(1999, 2006, 2013), except for *Dichanthelium aciculare* (Desv. ex Poir.) Gould & C.A. Clark, *Facelis retusa* (Lam.) Sch. Bip, and *Panicum hallii* Vasey var. *filipes* (Scribn.) Waller. Lichen taxonomy follows the USDA PLANTS database (USDA-NRCS 2015), except for *Dermatocarpon* a*renosaxi* Amtoft. We visited each study site twice, once in the spring and once in the summer of 2012, to capture early and late-blooming species. Species lists were combined from both visits to produce a single species list for each site. To quantify biological soil crust communities, we estimated total terricolous cryptogam cover and cover of three terricolous cryptogam morphological groups (fruticose lichens, foliose lichens, and mosses) in five 0.25-m^2 quadrats that were evenly spaced throughout the plot. We calculated mean plot-level values for each crust variable by averaging data from the five quadrats.

Soil Analysis. We collected soil samples from six evenly spaced locations throughout each plot and homogenized them before analyzing for organic-matter content, texture, and pH at Brookside Laboratories (New Knoxville, OH). We used organic matter to represent soil-resource availability in analyses because it is strongly related to both soil water-holding content and nutrient availability (Hudson 1994, Laughlin *et al*. 2007), and it has been shown to relate to species richness in dolomite glades (Miller *et al*. 2015).

Statistical Analysis. To analyze the effects of soil-resource availability on vascular plant species richness and total soil crust cover, we regressed each of these variables on soil organic-matter content. We also regressed vascular plant species richness onto lichen cover to test whether they were negatively related. We regressed the proportion of annual vascular plant species (of total vascular plant species richness) onto soil organic matter and onto topographic slope to test whether community life-history traits shifted in response to soil harshness and landscape position. We regressed soil organic matter onto topographic slope to test whether soil resource availability was related to landscape position. We natural-log–transformed soil organic matter, square-root–transformed average soil crust cover, and log-10–transformed topographic slope for analyses to improve their distributional properties. All variables met model assumptions of homogeneity of variance and normality (after transformation, if needed). All analyses were performed in R software (R Core Team 2014; R Foundation for Statistical Computing, Wien, Austria).

Results. We found a total of 96 vascular plant taxa across the 10 sandstone-glade study plots (Table 2), and species richness ranged from 16 to 37 within individual plots. Annual plant species ranged from 34% to 52% of total vascular plant species richness.

Average soil crust cover ranged from 0% to 80% (median 30%). Moss was the dominant component of the crust at some, but not all, sites, ranging from 0% to 75% average cover (median 6%). Fruticose lichens were also a dominant component of crusts, ranging from 0% to 43% average cover (median 10%). Foliose lichens were less abundant, ranging from 0% to 20% average cover (median 2%).

Soils were generally sandy, not surprisingly, ranging from 42% to 93% sand content. Soil pH varied little, ranging from 4.8 to 5.0. Organic matter content ranged from 1.4% to 6.3%, representing a range from low to moderately high values in comparison to other Ozark community types (Miller *et al*. 2015). Topographic slope ranged from zero (flat) to 18°.

Soil resource availability was strongly related to cryptogam cover and vascular plants species richness (Fig. 2). Vascular plant species richness increased with increasing soil organic matter ($R^2 = 0.40$, $P = 0.049$), whereas soil crust cover decreased as soil organic matter increased ($R^2 = 0.46$, $P = 0.031$). Vascular plant species richness and soil crust cover were negatively correlated ($R^2 = 0.43$, $P = 0.039$). Vascular plant species richness trended positively ($R^2 = 0.38$, $P = 0.059$) and soil-crust cover decreased ($R^2 = 0.54$, $P = 0.015$) with increasing topographic slope. Soil organic matter was greater on steeper slopes ($R^2 = 0.4$, $P = 0.049$). The proportion of annual plant species in the community decreased as soil organic matter increased ($R^2 = 0.57$, $P = 0.011$). Several annual vascular plant species that appeared to be adapted to the harsh conditions of shallow soil areas of sandstone glades occurred at almost all sites but varied substantially in abundance. Perennial vascular plant species occurred frequently at sites with soils with greater organic matter content but were less common at sites with harsher soils.

Discussion. Our study provides evidence that soil characteristics exhibit substantial influence on

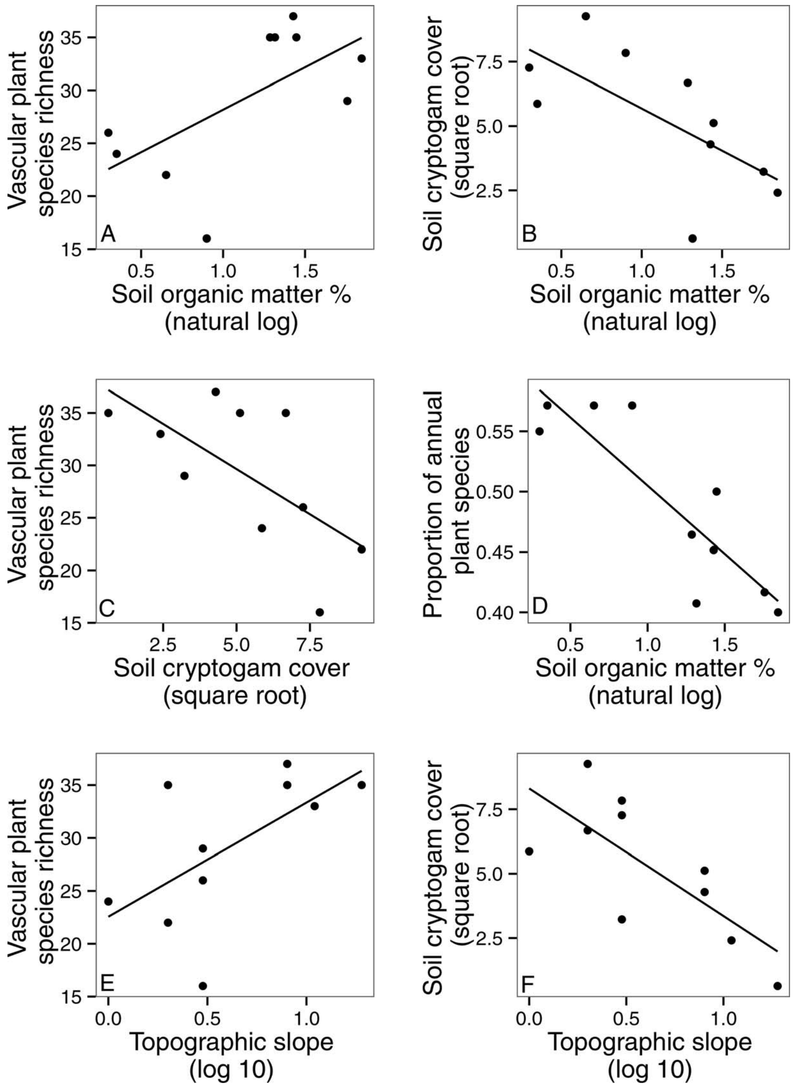

FIG. 2. Scatterplots showing relationships between (a) soil organic matter and vascular plant species richness, (b) soil organic matter and soil cryptogam cover, (c) soil cryptogam cover and vascular plant species richness, (d) soil organic matter and the proportion of annual plants in the community, (e) topographic slope and vascular plant species richness, and (f) topographic slope and soil cryptogam cover. All relationships are significant ($P < 0.05$) except for (c), which represents a trend ($P = 0.059$).

variation in plant and cryptogam communities among glades. As soil resource availability increases, soil crust cover and the proportion of annual vascular plants decreases, whereas the proportion of perennial vascular plants increases. Soil resource availability appears to be related to soil depth in glades, with greater organic-matter content in deeper soils (J.E.D.M., personal observations). These results suggest that soil crusts reach dominance in areas of glades with soils too harsh for perennial vascular plants to be abundant. Although we did not explicitly examine within-glade variation, previous work has shown that vascular plants and cryptogams respond to fine-scale variation in soil characteristics in this system as well (D. L. Jeffries 1985). Thus, it appears soil structures variation in sandstone glade plant communities at multiple scales. Our study is among the first to study sandstone glade communities at a regional scale, but our capacity for inference was still limited by a relatively small sample size. Ozark sandstone glades are ripe for further research examining both fine-scale vascular plant-soil crust interactions and broad-scale biogeographic patterns.

Sandstone glades are naturally heterogeneous environments, with soil depth typically varying significantly over distances of a few meters. However, the relative abundance and size of shallower and deeper soil patches varies among glades (J.E.D.M., personal observations). A few vascular plants are ubiquitous across our study sites and occur in areas of harsh, low-fertility soils among patches of lichen and moss crusts. These tended to be annual species that complete their life cycles before the hot, dry days of late summer (*e.g.*, *Croton wildenovii* G.L. Webster and *Oenothera linifolia* Nutt.) or succulents that are able to tolerate periods of intense environmental stress (*e.g.*, *Phemeranthus calycinus* (Engelm.) Kiger and *Opuntia spp*.). Sites with greater average soil organic-matter content still generally contain the above-mentioned stress-adapted species in shallower soil zones but also contain additional species in deeper soil zones. The identities of these species are more variable than the predictable assemblage of shallow-soil species, and they include numerous perennial species that are apparently intolerant of the harshest glade soils. Several of these species typically occur in grasslands that have more-fertile soils than sandstone glades, such as dolomite glades and prairies. Glade soils with greater organic matter content are probably able to support larger-statured, perennial plants because they are deeper, hold water more effectively, and have greater nutrient availability.

Previous research has shown that fine-scale substrate variation can have strong effects on glade communities. Quarterman (1950) classified limestone cedar glade plant communities along a gradient of harshness related to soil and rock and identified a spatial (and putatively successional) shift from cryptogam-dominated communities in the rockiest areas to vascular plant guilds as soil depth increased. Many of the community types that Quarterman (1950) recognized are reminiscent of Ozark sandstone glades communities. Previous research in Ozark sandstone glades has found that soil pH varies substantially at a local scale and has strong effects on local plant communities and cryptogam dominance (Jeffries 1985, 1987). However, we find that the average soil pH among glades varies little (from 4.8 to 5.0), perhaps because of the scale at which we examine communities (*e.g.*, combining multiple soil samples from within sites for analysis). Instead, soil organic matter and topographic slope, which are positively correlated, both vary considerably among our sites and are associated with changes in plant and soil crust communities. Steeper glades have better-developed soils than flat-rock glades had, with more grass-dominated, prairie-like plant communities. Although Jeffries (1985, 1987) sampled both flat rock and steeper glades and measured slope and organic matter, there is no discussion of the role of topography or soil organic matter in influencing plant communities, perhaps because the focus is on variation within glades (or glade complexes) rather than variation among glades. Research in Ozark dolomite glades, however, similarly found positive relationships among topographic slope, soil resource availability, and plant species richness (Miller *et al*. 2015).

In arid and semiarid regions, soil crusts are often associated with high-quality, native plant communities, perhaps because crusts and vascular plants have common responses to land-use legacies associated with habitat degradation, such as intensive grazing (Maestre *et al*. 2011, Root and McCune 2012). In contrast, in wetter regions, soil crusts can be either negatively or positively related to native plant richness (Sedia and Ehrenfeld 2003, Langhans *et al*. 2009, Soudzilovskaia *et al*. 2011). Our work suggests that soil crust cover may be inversely related to vascular plant richness when the plants and crusts in question have varying resource requirements that correspond to a steep, local, environmental gradient. Conversely, when large-scale factors, such as climate, limit the productivity and competitiveness of vascular plants—as in arid regions—it may be easier for vascular plants and soil crusts to coexist at multiple scales. Future experimental research could test whether there are zones of intermediate soil depth in sandstone glades in which either vascular plants or crusts could achieve stability—a pattern that is documented in other systems (Sedia and Ehrenfeld 2003). Although total crust cover does not appear to be associated with areas of high plant richness in Ozark sandstone glades, it is still possible that certain crust-forming, cryptogam species or functional groups could be associated with high vascular plant species richness. For example, some crust species could be indicators of land-use history, which may also influence glade plant communities (Nelson 2005). We observed that terricolous *Dermatocarpon arenosaxi* was abundant at only two glade sites that had particularly rich vascular plant species.

Crust-forming lichens in sandstone glades are diverse but poorly studied. Identifying all lichens to species was beyond the scope of this study, but inventorying glade lichens should be a focus of future research. In particular, better documentation of distributions of rare species (*e.g.*, *Psora icterica* (Mont.) Müll. Arg. and *Pycnothelia papillaria* (Ehrh.) L.M. Dufour), and the influences of the local environment on lichen diversity would be useful to managers, who generally have little access to information about glade lichen communities. Significant progress has recently been made in understanding distributions of rare soil crust lichens in areas of the arid west (Miller *et al*. 2011, Root *et al*. 2011, Root and McCune 2012), which were previously little studied, and similar work for soil crusts in the Ozarks and other little-studied areas in eastern North America would help us better understand and manage these organisms.

Management Implications. Sandstone glades face multiple management challenges. Feral hogs represent one considerable threat to glade communities and can cause substantial damage to sensitive soil crusts (J.E.D.M., personal observations). Protecting these glades from such disturbance will be increasingly important as hog populations continue to increase in the region.

This study highlights the importance of conserving sandstone glades across a gradient of soil conditions. Numerous plant species of conservation concern are adapted to shallow soils in sandstone glades; for example, *Geocarpon minimum* generally occurs along the margins of bare rock exposures (Smith and Ely 2006). Remnant sandstone glades with well-developed soil also contribute a unique element to the sandstone glade flora and should be a focus of conservation concern. Glades with well-developed soil are at a greater risk from encroaching woody vegetation than are glades with harsher soils in which woody plants cannot readily establish (Miller *et al*. 2015). Many historically open grassland areas in and around sandstone outcrops in the Ozarks have probably been fully converted to wooded structure, just as similar deeper soil grasslands have been lost from the matrix surrounding the limestone cedar glades of Tennessee (Albrecht *et al*. 2015). Using fire as a management tool is crucial for maintaining the open structure, biodiversity, and connectivity of glades (Templeton *et al*. 2001). Glade areas with very shallow soil, although more resistant to encroachment, still benefit from the landscape effects of fire (Heikens 1999, Maurice *et al*. 2004).

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