Grasshoppers, Glades, and Ecological Gradients

Plant communities, herbivory, and fire regimes in the Ozarks inform new ecological thinking

By Jesse E. D. Miller, PhD

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Plant communities in Ozark glades, such as Rockytop Glade at Lake of the Ozarks State Park, support diverse grasshopper communities.

On a warm August afternoon, strolling through a dolomite glade in the heart of the Ozarks, it's hard not to notice the hum of activity as grasshoppers flit around amid the bluestem and Missouri coneflowers. Although I didn't give much thought to the grasshoppers when I first started working in Ozark glades, I soon noticed that their voracious appetites sometimes extended beyond plant tissue: the PVC pin-flags I left to mark my study plots would inevitably have pieces bitten off by little grasshopper mouths. As I talked to other glade biologists, I learned this was a common theme: the grasshoppers seem to eat whatever comes across their paths. So perhaps it is no surprise that grasshoppers play a significant ecological role in warm-season grasslands, and their population dynamics seem to be intimately connected to the plant community as well as management activities. Today, at least, with bison generally extirpated, grasshoppers might be considered the dominant herbivores in our warm-season grasslands. Nonetheless, ecologists tend to overlook these cryptic plant eaters and their role in ecosystems, much as I had when I started my work in the Ozarks.

The Maturation of Ecology

Ecology is a relatively young discipline, and much of what we understand today about how plants and animals are distributed across landscapes, bioregions, and continents has been learned in recent decades. In the first half of the 1900s, influenced by the work of Frederic Clements, many ecologists saw natural communities as "superorganisms"—predictable assemblages of species with discrete boundaries, relatively unchanging in composition at each location where they occur on a landscape. It wasn't until the 1950s that Robert Whittaker showed the first conclusive evidence that plant communities change gradually along environmental gradients—for example, along a gradient from wet to dry habitats—which today seems so basic and intuitive to most ecologists that it's hard to imagine a time when it wasn't generally accepted.

It wasn't until quite a bit after Whittaker's time that ecologists came to fully appreciate the influence animals can have on plant distributions, and vice-versa. Today, scientists recognize a complex and dynamic interplay between plants and the animals that eat them. Plants make a remarkable number of compounds that deter herbivores (by tasting bad or being poisonous). The quantities of these chemicals in plant tissues can vary greatly between and within populations of a single plant species, and even vary substantially over time within an individual plant (as in herbivore-induced defense, where a plant produces more defense compounds in response to being eaten). We have also learned that animals can significantly change plant communities—something that was not generally recognized in Whittaker's time. For example, recent research in Wisconsin shows that deer overpopulation has led to declines in rare lily and orchid species.

Much of the previous research on plant-herbivore interactions has taken place at local scales (e.g., studies focused on one or a few individual plants), and often in experimental settings. Less is known about how local plant-animal interactions scale up to affect diversity patterns at broad scales, such as across a landscape. Studies from many ecosystems have shown, however, that there is often a positive relationship between plant and herbivore diversity. That is, a site with high plant richness (total number of different plant species) tends to also have a high richness of herbivore species. Two potential explanations for this pattern have been advanced, although scientists have yet to test them extensively in natural systems. The first explanation is that plants and herbivores could both respond similarly to environmental conditions. For example, it's conceivable that plants and herbivores could both be more abundant at sites that are less environmentally stressful, simply because these sites have better conditions for both plants and herbivores. Alternatively, the second explanation for positive plant-herbivore diversity relationships is that herbivores derive some kind of direct benefit from more diverse plant communities, and this leads to greater herbivore richness. While these two explanations are not necessarily mutually exclusive, understanding their relative importance will ultimately help ecologists explain patterns of biodiversity in natural landscapes.

Tracking the Glade Grasshopper Story

After my first long season in the Ozarks studying plant communities in glades in 2012, I became curious about interactions between glade plants and the abundant

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At top, Phil Hahn uses a sweep net to collect grasshoppers at a study site in the Bay Branch drainage in Angeline Conservation Area, Shannon County, MO. Above, a spur-throated grasshopper (*Melanoplus bivittatus*) in a dolomite glade.

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Clockwise from left are the Ozark dolomite glade endemic, Ozark coneflower (*Echinacea paradoxa*), blooming at Ha Ha Tonka State Park in Camden County, MO; a sweeping view of Ava Glades Natural Area, Mark Twain National Forest, Ozark County, MO; and pale purple coneflower (*Echinacea pallida*) and Trelease's larkspur (*Delphinium treleasei*) at Chute Ridge Glade, Mark Twain National Forest, Barry County, MO.

grasshoppers that dominate the glades in late summer. This interest was inspired in part by my colleague Phil Hahn, an insect ecologist and fellow graduate student at the University of Wisconsin-Madison at the time. Over the long Wisconsin winters we discussed ecological matters while we sipped good ale and gazed out over the frozen lakes of Madison, which appear a bit like winter grasslands when the light is right.

Through these conversations, we hatched a plan to study patterns of grasshopper diversity in a network of Ozark dolomite glades where I had already begun documenting plant diversity patterns. I had previously discovered that glades vary greatly in soil fertility, and there was also substantial variation in the fire histories of these glades because they were burned at different frequencies. Thus, the stage was set for teasing apart the two potential explanations for plant and herbivore diversity relationships that have long eluded ecologists.

To assess grasshopper and plant diversity patterns, in 2013, Phil and I visited 15 of the study plots I had previously established in dolomite glades. We made our visit in August, since late summer is when grasshoppers generally reach greatest abundance. All the sites we selected are considered intact glades by managers. There was no significant difference in the mean plant coefficient of conservatism (a measure of plant affinity to intact natural conditions) among our glade study sites, although the sites varied substantially in plant richness.

I had established long, skinny, rectangular study plots in which I recorded plant composition in these glades (a modification of Robert Whittaker's original vegetation sampling protocol, in fact), and Phil walked up and down the edge of the plots using a sweep net to collect grasshoppers from vegetation. This is considered the most reliable way to study grasshopper communities—like other insects, grasshoppers generally have to be collected for identification, since they will fly away before they can be identified visually in the field. I also resurveyed the plant communities on these visits.

We froze the grasshoppers for storage and then, over the long Wisconsin winter, an undergraduate, John Brennan, helped with the tedious task of sorting grasshoppers from the vegetation debris that made up most of the volume of our collections. Phil then identified the grasshoppers, and we assembled a database containing fire histories and soil characteristics of each plot.

Herbivore and Plant Richness Relationships

There was a great deal of variation in grasshopper richness across the glades we sampled—ranging from only three to 15 species, and plant richness also varied substantially, from 14 to 62 species. As we expected, there was a strong positive relationship between plant and grasshopper richness.

Plant and grasshopper richness, however, did not respond to the same environmental gradients. Plants responded strongly to soil fertility, with plant richness increasing with increasing soil organic matter content. Grasshoppers did not respond directly to soil characteristics, though their response to the plant community can be considered an indirect response to soil characteristics.

Grasshoppers did, however, have a strong response to glade fire histories. Grasshopper richness was substantially lower in glades that had burned more recently, and it appeared that grasshoppers take several years after fire to return to "unburned" diversity levels. (Paradoxically, grasshoppers, like many grassland butterflies, are both fire sensitive and fire dependent because of their survival's linkage to an herbaceous plant community.) Overall, these results indicate that plant richness directly affects grasshopper richness—a finding that, while not particularly surprising, represents one of the first documented cases of herbivore richness being functionally or directly dependent on plant richness in a natural system.

There are a few potential explanations for how plant richness could affect grasshopper richness. Greater plant richness means a greater diversity of plants that can be eaten. Grasshoppers vary quite a bit in their dietary preferences and degree of specialization—some grasshopper species specialize on grasses, while others also eat forbs. A wider range of plants available for forage could support a greater variety of grasshoppers with unique diets.

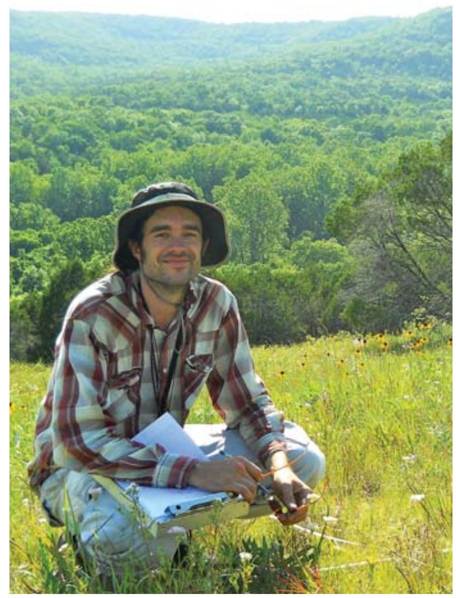
Greater plant richness may also mean more diversity in plant architecture, and glades with high plant richness tend to have more tall plants. Such variation in plant structures could provide a more complex habitat that supports more species, and might also allow grasshoppers to better hide from predators. Glades with high plant richness generally have higher plant biomass as well, because both plant richness and biomass increase in more fertile soils. We considered the possibility that it could actually be plant biomass, rather than species richness per se, driving grasshopper richness. To test whether this could be the case, we quantified productivity (i.e., plant biomass) for each glade using remotely sensed imagery. There was not, however, a significant relationship between productivity and grasshopper richness, suggesting that plant species richness does directly confer greater grasshopper richness independent of productivity.

Conserving a Broad Spectrum of Glade Communities

Glades are a fascinating system with a rich natural history, and there is a great deal more to be learned from studying them. The scope of this observational study did not allow us to test the possibility of reciprocal relationships—the idea that plants and grasshoppers are influencing each other simultaneously. While we tested only plant effects on grasshoppers here, it is likely that grasshoppers have some influence on plant species composition and abundance as well. Grasshoppers feed selectively on different plant species, and this could decrease or eliminate some plants while favoring others by reducing competition. In addition, more work will be needed to understand exactly what the interactions that link plants and grasshoppers are. Phil and I plan to address some of these questions in the future.

In the big picture, one important lesson from this study is that there is a great deal of variation in plant and animal communities among different glades, and especially among glades with different soils and fire histories. Since the variation in soil fertility that we observed seems to be linked to topography and soil type, and has probably existed for millennia, the variation in plant and grasshopper species richness and composition that we observed has probably been present in this system for a long time. Conservation management often focuses on local diversity (e.g., species richness), but our findings highlight the great extent to which variation in species composition across the landscape (also called species turnover or beta diversity) contributes to regional diversity. To conserve the great biodiversity of glades, it is necessary to conserve numerous individual glade complexes representing the entire spectrum of plant and grasshopper species composition. This brings us back to some foundational ideas of ecology.

Frederic Clements' "superorganism" concept of ecological communities as fixed, discrete assemblages has remained influential in conservation planning despite being widely rejected by ecologists for decades. At its extreme, this worldview purports that there is a single "ideal" species composition in a given system (e.g., in a dolomite glade). In contrast, our research shows that glades with high floristic quality can take a number of different forms, with varying species composition. Fortunately, we are lucky to have a large, active and forward-thinking conservation community in Missouri that embraces modern ecological thought. Indeed, numerous agencies and organizations that manage glades in the Ozarks are collectively conserving glade landscapes across a broad range of community composition.



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Jesse E. D. Miller (above) spent several years studying plant communities in Ozark glades for his dissertation research at the University of Wisconsin-Madison. He is now a postdoctoral researcher at the University of California, Davis, but plans to continue research in Ozark glades intermittently for the foreseeable future. Philip G. Hahn, who contributed equally to all aspects of the study described here and provided assistance with this article, is a postdoctoral researcher at the University of Montana. Any comments or questions about this article would be appreciated, and can be sent to Jesse at kawriver@gmail.com. To read the scientific paper Miller and Hahn et al. wrote on this study ("Functional dependence underlies a positive plant-consumer richness relationship," Basic and Applied Ecology, 2017), as well as Miller's other glade research, please visit jesseedmiller.com/publications.
The author and colleagues are very grateful to the many Ozark land managers, ecologists, and botanists who helped make this study possible, and to the many agencies and other landowners that allowed us to sample on their glades.