

Image 1. Historically, the wet bottomland prairie at Pershing State Park offered a colorful display of yellow, purple, and white forbs in the fall, including various species of *Bidens*, *Symphotrichum*, and *Boltonia*. This photo was published in a two page spread in *The Terrestrial Natural Communities of Missouri* (Nelson, 2010) as the representative illustration of wet bottomland prairie.

A Prairie Persists: A Tale of Resilience and Loss in a Wet Prairie System

by Carrie Stephen

Pershing State Park sits tucked away off Highway 36 in Linn County, Missouri. It is an easily overlooked gem as you drive by, holding remnant fragments of a historically diverse system of wet prairie, bottomland forest and shrub swamp. In the floodplain of a once wild, meandering Locust Creek, several sloughs, marshes, and oxbow lakes persist. Locust Creek was a life source for these diverse communities. Today, within the park's boundary, Locust Creek is all but dry most of the year. It is only with the help

of some human engineering that the wet prairie that persists can see recharge without immense sediment loads. The story of the wet prairie at Pershing is not a particularly happy one, but it is important to share. What is shared here is just a fragment of the story. Wet bottomland prairies, ranked Critically Imperiled in Missouri, are rare among prairie types. Prairies as a whole are already grossly reduced compared to their historical extent. And so the fervent mission to save the wet prairie at Pershing SP continues (Image 1).

Pershing's wet prairie communities were not initially recognized for the splendor they possessed at the time the park was created in 1937. Pershing primarily exists from the wake of World War I when local residents wanted to honor their own Linn County original, General John J. Pershing, and his service during the war, with a national park. When the National Park Service declined the nomination, citizens recommended a state park which was pursued by the state of Missouri. At the time, the natural beauty of the park was recognized in the majestic cottonwoods in the bottomland forests and in the meandering Locust Creek, a disappearing natural feature in North Missouri as prevailing forces in the largely agricultural interface favored channelization. However, the wet prairie systems at the time of designation as a park were largely overlooked.

The wet prairie was dismissed to the degree that in the 1970's, a local park manager "put the treeless ground to good use" by row cropping it for two years. Persistent flooding from Locust Creek quickly ended the venture. Fortunately, the prairie survived and healed from this effort, and the area was soon after recognized as a good quality wet bottomland prairie by the then-nascent Natural History Program. At over 700 acres, it was the largest known wet prairie remaining in north Missouri.

By the time the wet prairie was recognized as possessing botanical value, it was likely already undergoing degradation from its historic state. The wet prairie suffered not only from a brief attempt at farming, but also from the early impacts of sedimentation and artificial retention of flood waters because of the levee system surrounding it. However, in the spring, a rich grass and sedge community dominated, particularly after a prescribed fire. The plant communities varied with minor topographic and subsequent moisture differences. Closer to

Floods of 1993 Impacts to Pershing State Park

The summer of 1993 saw catastrophic rainfall throughout the Midwest. All time high flood stage records were broken along the Missouri River from Kansas and Nebraska to St. Louis, Missouri. On July 10, the Grand River crested at a record 42 feet at Sumner, 20 miles north of the river's confluence at the Missouri River. Flood waters from the Grand backed up 5 miles to Pershing State Park, inundating the Locust Creek floodplain. These murky floodwaters persisted for at least 30 days, covering the bottomland prairie and forest in water at least 6 feet deep. Adding to the flow event, Linn County received 14 inches of rain in July. As the waters finally receded, park ecologists observed that much of the once vibrant cover of prairie grasses, sedges, and forbs had succumbed in the month of silty, dark-standing water. Foul decay of dead vegetation followed during the summer heat. Because the Missouri River floodplain is largely covered in levee systems, this flood event was deemed unnatural. In addition, the levees surrounding the wet prairie likely contributed to unnatural retention of the floodwater. Ecologists feared that this event dramatically reduced or eliminated much of the natural distribution of prairie plant species.

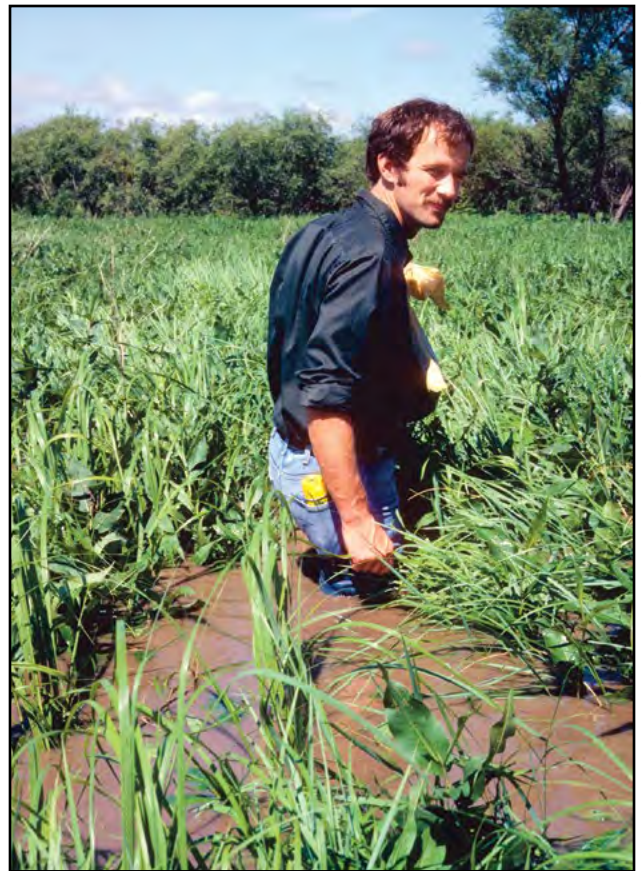
the creek, a wet mesic prairie displayed compass plant (*Silphium laciniatum*), goldenrods, asters, and sunflowers. Along Locust Creek, a community of bottomland forest also housed great sedge, grass, and forb diversity.

Early on, prairie management explored methods on how to reintroduce fire to such a wet area. Ultimately, managers determined that fall and early winter burning was the most effective before snow pack and spring moisture affected fuel. Other early projects involved pushing back on woody encroachment from the treeline. In the late 1980s and early 1990s, no one involved in ecological management in the area realized the extent of future challenges.

The story of Cordgrass Bottoms Natural Area

At the time of the park's establishment, Pershing was actually home to two wet prairies. In 1979, Cordgrass Gumbo Prairie-Marsh, a 76-acre wet bottomland prairie, was nominated as the Cordgrass Bottoms Natural Area. The original nomination listed cordgrass, water smartweed, wild water pepper, and cutgrass as the dominant plant species. Other noted flora included bugleweed, common ironweed, water parsnip, blue flag iris, swamp milkweed, false aster, and a variety of sedges (such as *Carex grayii* and *Carex hyalinolepis*). Unfortunately, this prairie did not persist throughout the years—instead, through time, it was buried by several feet of sediment due to unnatural flood events from Locust Creek. Among the few photos that remain of historic Cordgrass Bottoms is of then-Chair of the Missouri Natural Areas Committee and Director of the Natural History Program from Missouri State Parks, Paul Nelson, standing knee high in cordgrass and sedges during a flood pulse on Locust Creek (Image 2). During 30+ years of sedimentation, cordgrass disappeared from the natural area as it morphed into a doghair thicket of silver maple and reed canary grass. The Committee delisted Cordgrass Bottoms NA in 2014 as the defining feature of wet prairie no longer existed.

Historically, Locust Creek was the lifeblood of the wetlands at Pershing State Park. Due to upstream channelization, land clearing, and row cropping into the riparian corridor, Locust Creek began carrying an excess of logs and sediment, which had become the largest threat to these complex wetland systems. By the late 1980s, ecologists with Missouri State Parks began to note issues that come part and parcel with excess sedimentation. In the 1990s, the Missouri Department of Natural Resources began a strategy of acquiring land to create buffers to filter and trap sediment in the streambed, with the intention of preventing intense sedimentation



Missouri Department of Natural Resources file photo

Image 2. This 1979 photo shows former Natural Areas Coordinator, Paul Nelson, with a collecting bag of sedges in Cordgrass Bottoms NA during a flood event. This natural area was delisted in 2014 as the wet prairie no longer exists and today the area is a thicket of silver maple and smartweeds, supported by excessive sediment.

further downstream where remnant wetland communities still thrived. Although this strategy was well-founded, land acquisition was a slow process. By the late 1990s, sedimentation grew to a severe problem.

Sedimentation and log jams at Locust Creek

The threat of sediment loading is three-fold. In the forefront is the sheer amount of sediment traveling downstream to the park. Heavy erosion upstream results in significant sediment loads that bury native vegetation. This amount of sedimentation also homogenizes topographic diversity, which affects moisture gradients and resulting plant communities. Second, the high levels of sedimentation build ground quickly,



Missouri Department of Natural Resources file photo

Image 3. Bottomland forest filled in with sediment after a major flood event. Vegetation has been completely buried. Prior to flooding, these forests hosted diverse flora including spring wildflower displays and Pale Green Orchid where the forest edge met the wet bottomland prairie. The pale green orchid population was lost due to 2 feet of sediment deposition.

such that creek dynamics change more drastically than before. One major change is that the creek bed continues to rise due to sedimentation, which then creates pressure upstream and a greater possibility of flow diversion away from the original creekbed. A 2013 U.S. Army Corps of Engineers (USACE) study on the Locust Creek Watershed estimated that Locust Creek had risen between 2 and 4.5 feet between 1974 and 2013. In 2017, monitoring determined that the Locust Creek channel sits higher than most of the floodplain around it. Because of the amount of sedimentation, the channel continues to rise more quickly than in the past. Third, sediment loads bring in nutrient flushes which cater to a different community of vegetation—weedier species such as invasive reed canary grass.



Missouri Department of Natural Resources file photo

Image 4. Wet bottomland forest at Pershing State Park hosted moderate vegetative diversity prior to excessive sedimentation. Flora included ostrich fern and various sedges with an overstory of large cottonwoods, oaks, and silver maples. Indiana bats have also been found in this forest. The trees remain, but much of the flora has been lost.

Sedimentation has affected all of the wetland systems at Pershing State Park, including the former Cordgrass Bottoms NA, the 700-acre wet-mesic and wet bottomland prairie further south in the park, the bottomland forests, and the shrub swamps (Image 3). The park lost its only known population of the state species of conservation concern pale green orchid (*Platanthera flava* var. *flava*) in the 1990s after a large sedimentation event (Image 4). The location of that population sustained a 2 foot load of sediment, and the orchids have not been seen since. The sheer quantity of sediment over time is difficult to overstate. For example, at Locust Creek Covered Bridge State Historic Site, the current foundations for the bridge are 14 feet higher than the original foundations. The

foundations of the bridge were raised multiple times because of the sedimentation. Today, the covered bridge rests squarely on solid ground of what was once the creek. Plans are underway to relocate the historic site to a more sustainable location. Sedimentation also buried a remnant wet prairie, known as the Massie tract, owned by The Nature Conservancy and leased to Missouri State Parks to add to the larger wetland matrix at Pershing. Both before and during mitigation efforts, an entire wetland mosaic has lost a great amount of its diversity due to years of repeated sedimentation events.

Because Locust Creek meanders through Pershing, though is channelized north of the park, Pershing also finds itself the location of numerous log jams. Small log jams were part of the park's history for a long time and had not caused significant issues downstream in the park. When the first major log jams appeared at the park in 1993 shortly after the historic Mis-

souri River floods, management viewed these as a natural part of the creek system. In a previous landscape with a gentler anthropogenic influence, these log jams were normalized as a natural function of the system. Over several years in the 1990s, park management grappled with public opinion on removing the logs, as large logjams affect flooding and farmland in the larger watershed. During that investigation period, the creek adjusted in sections of the log jam on its own—it meandered around or sometimes through the logjams, and deposited sediment on top of the logs which quickly filled in with vegetation, and formed a new channel.

By 1995, with more flooding impacts, more logjams accrued further north in Locust Creek. Although the creek adjusted to the logjams and sediment loading in some sections, other areas became more severely plugged and did not have any clear path for the water to run around or through (Image 5). During a high flow event in

Image 5. A logjam has filled Locust Creek from bank to bank in 2021. This log jam began accruing in 2019 and by 2021 extended for 1.25 miles. Work on this particular log jam began in 2021 and continues today.



Photo provided by Dustin Webb, Missouri Department of Natural Resources

the creek, log jams rerouted overflow directly through the bottomland forests and into the wet prairie. The high flow event filled the sloughs and other wet depressions with sediment, and with the sediment came reed canary grass and other undesirable vegetation. Sections of bottomland forest and wet prairie were buried. This was a historic turning point for how the park would address future log jams and the threat of immense sediment loads. With the amount of erosion occurring upstream due to changing land use practices, the park no longer felt that the creek and surrounding wetland systems could accommodate the number of log jams, the speed at which they grew, and the immense sediment loads without great risk of losing the wetland systems all together. Thus in 1996, the park staff began managing logjams.

Early on, logjam management was primarily conducted with bank-packing. The park modeled the technique after observations of what the creek does on its own, but aimed to speed the process up to prevent a repeat of high flood events depositing large sediment loads in the bottomland forests and wet prairie. That is, park staff packed logs into the inside of creek bends to create point bars and thus formed a pilot stream on the outside which the creek itself then widened. By utilizing the inside of creek bends, the creek would naturally deposit sediment on the log debris, which encouraged vegetative growth. Sediment and vegetation together helped lock point bars in place. This method met some resistance early on, particularly with concerns over whether the logs would remain locked in place in the constructed point bars. Ultimately, the point bars were successful and continued like natural point bars, and thus re-vegetated relatively quickly.

Throughout the 1990s and into the early to mid-2000s, bank-packing was the method the park used to address log jams. But the log jams kept coming, new channels kept forming, and more sediment was depositing. Managing log-

jams became a major challenge. Additionally, sedimentation was causing the creek channel to rise. These two facets of ecological issues applied pressure to upstream flows, slowing down the upstream flow. Consequently, Locust Creek naturally did what any creek would do when faced with a massive plug—reroute to an easier path. This reroute took Locust Creek and much of its flow to Higgins Ditch.

Higgins Ditch is a straight channel, created by farmers in the area to drain their crop fields during flood events long before massive logjams started to plague Pershing. It lies less than three quarters of a mile west of Locust Creek where they both pass under Highway 36. The wet prairie lies in between Locust Creek and Higgins Ditch south of the highway. Amidst the monitoring, debating and scrambling to remove the many log jam problems along Locust Creek, water found an easier route and began to head cut towards Higgins Ditch just north of Highway 36. Park managers noted their concerns early on, when the headcut was quite small, but the evolution of the headcut to a complete reroute of the creek was swift—at least faster than the park could respond. With subsequent high flow events and logjams, Locust Creek completed its path to Higgins Ditch. At that point, large amounts of flow were pirated away from the original Locust Creek on a regular basis. With that pirating, flood events (with excess sediment) were also a threat from Higgins Ditch.

To be clear, the headcuts likely began with early sedimentation and before the first major logjams. But subsequent and rapid accumulations of logjams greatly sped up the process. Efforts were made early on to prevent water pirating to Higgins Ditch. Park managers installed gradient control structures in 2007 to restore flow to the original creek. Although these structures were relatively effective early on, the pressure they had to withstand was trying, and park managers realized quickly they would need to continue taking action. In 2009, park

staff notched some levees to relieve pressure on the gradient control structures. In 2012, with the help of some grant dollars, MDNR added several more gradient control structures. However, at a certain point, yet another log jam formed at these structures and that, combined with record flooding, compromised their functionality. A tipping point was reached, and the cut-across channels quickly became the new primary path of Locust Creek. The bulk of that water flowed directly into Higgins Ditch, leaving the original channel of Locust Creek all but dry. In 2010, it was determined that Locust Creek channel sat over 10 feet higher than the Higgins Ditch channel. With this difference in elevation, maintaining flow in Locust Creek has proven to be a losing battle.

Consequences of the loss of flow in this section of Locust Creek affect species beyond the terrestrial wetland communities around the creek. The flat floater mollusk (*Utterbackiana suborbiculata*) and trout perch (*Percopsis omiscomaycus*) were both species that have lived in Locust Creek within the park boundary. The flat floater is considered imperiled and the trout-perch is critically imperiled in Missouri. Since the creek has been pirated away, neither species have not been found within the park boundary. Locust Creek maintains a greater flow south of the park where tributary streams and creeks restore flow, and so these species may persist in other areas, but their habitat has certainly been diminished.

The story of Locust Creek Restoration Area and Locust Creek Wet Prairie

Although Cordgrass Bottoms was lost to sedimentation, Pershing has seen some successes in wetland management. To protect the larger wet prairie further south, MDNR partnered with the Natural Resources Conservation Service (NRCS) to create a buffer zone with land acquisition—an area that could filter out the large sediment loads while still allowing water to recharge the wet prairie. The goal was to restore this former soybean field to wetland to function

as an extension of the current wetland systems and provide additional habitat for wet prairie and marsh communities. With some additional federal funding, in 2009 MDNR purchased 1,449 acres divided into two units as a part of the Locust Creek Restoration Area project.

This land was historically used for agricultural production for years, and was located where it could absorb some of the sediment pulses that were coming from Higgins Ditch and Locust Creek. Together, NRCS and Missouri State Parks developed a wetland restoration plan, which involved engineering a flat agricultural landscape into a riparian floodplain. In the mid-2000s, MDNR and NRCS implemented the plan to construct berms and other structures to mimic oxbows, ridges, and swales so that floodwater could be guided through the system and thus mimic the historic wetland landscape. During flood events, this LCRA wetland allows for sediment deposition in the restoration area instead of in the wet prairie itself. Over time, with the cooperation of other land owners, some of the levees were dropped to allow water to sheet over them in a manner that would better replicate water flow in a floodplain. This sheeting also helped move sediment through the system without too much deposition in any one location.

Additionally, massive amounts of seeding and planting of cordgrass plugs have contributed to a vegetative restoration of the area. The restoration is maintained with fire to prevent woody encroachment. Because the area is essentially a sedimentation catchbasin during flood events, some areas favor a lot of weedy (and even invasive) species like reed canary grass, but as a whole, the restoration has offered an excellent opportunity for wetland habitat expansion. In fact, prairie massasauga rattlesnakes (*Sistrurus tergeminus tergeminus*), which have lived in the wet prairie for many years, have colonized the LCRA. Prairie massasaugas are state endangered, so the expansion of their habitat at the park has been an exciting affirmation of the success of the Locust Creek Restoration Area.

Overall, this restoration area offers protection for what remains of the wet prairie. The LCRA successfully filters sediment from high flow events in Higgins Ditch. As effective as LCRA is, the truth remains that the wet prairie is not the same as it was 30 years ago. Years of sedimentation have resulted in what seems like seas of reed canary grass encroachment and the reduction of many of the native grasses, sedges, and forbs that covered this area years ago, not to discount the impact of a teeming deer herd, managed annually with Managed Deer Hunts. Reductions in the herbaceous diversity from sedimentation and deer herbivory have impacted invertebrate and bird populations (Image 6). Still, pockets of that original wet bottomland prairie containing prairie cordgrass, bulrush, asters, and other various sedges continue to persist though in diminished populations.

Restoration efforts are not complete, and challenges remain. The wet prairie has lost its lifeblood from Locust Creek due to lack of flow. Although Higgins Ditch has, in the recent past, offered hydration as routed through LCRA, the ditch has deposited so much sediment in LCRA that flood waters no longer filter through the way they did upon original design of the wetland project. Instead, floodwaters remain channelized in Higgins Ditch or overbank in the western reaches of the park. Logjam projects continue—to date, MDNR has removed or treated at least 30,463 feet of logjams. The Department has spent over \$1.9 million on log jam projects, which does not include contributions from other agencies. These numbers continue to grow every year. Logs are now often removed, and not just packed into banks due to the quantity. Although the cost of removal varies, on average, it costs \$100/linear foot of logjam, which adds up quickly considering the park has addressed miles of log jams over the years.

The invasive common reed (*Phragmites australis* var. *australis*) has posed a new threat. While this species has not colonized the wet prairie, it grows



Photo by Carrie Stephen, Missouri Department of Natural Resources

Image 6. The impact of deer overbrowse on native forbs at Pershing leading to additional instability of the natural communities cannot be underestimated.

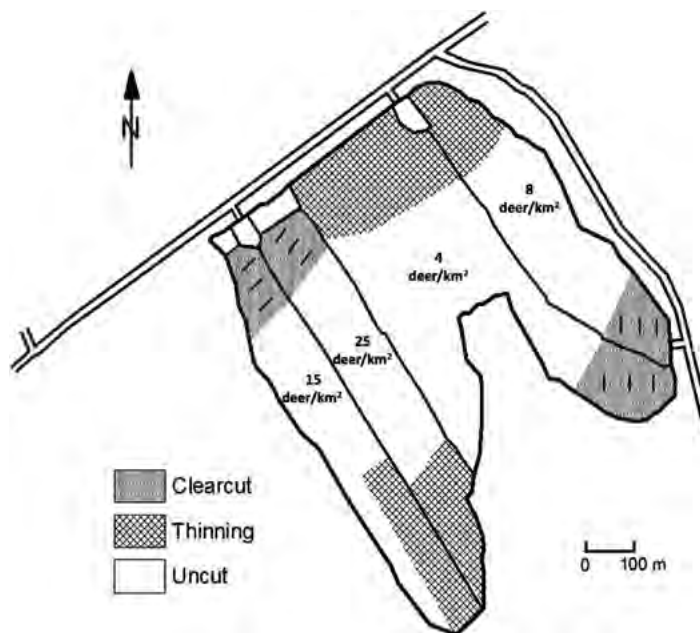
in the LCRA. Common reed is a challenging species to remove, although preliminary drone treatments have proven promising.

As overwhelming as the challenges can be, the wet prairie persists, and we are still trying to save it. Even without hydration from the creek, the soils still hold water well from precipitation, and those moisture-loving species have managed to continue to make their home there. Buttonbush still sticks out in the swales. Bulrushes stand tall. The cordgrass, sedges, iris, white beardtongue, false asters, saw toothed sunflowers, and obedient plants still persist in beautiful little pockets if one takes the time to find them. 🌿

Carrie Stephen is a Natural Resource Ecologist for the Missouri Department of Natural Resources.

Contact: Carolyn.stephen@dnr.mo.gov

Figure 2. Map of one of four deer enclosures showing the different deer density and forest management treatments with each line in the clearcut location representing a 30 × 5 m belt transect. Deer populations were maintained for approximately 10 years within the enclosure experiment (1989–1990). This study evaluated stand and canopy structure in the clearcut sections of each deer density treatment



2.2 FOREST SPECIES DIVERSITY, STAND STRUCTURE, & CANOPY STRUCTURAL COMPLEXITY

In June and July 2016, we measured forest stand structure, species composition, and canopy structure, approximately 36 years after stand re-initiation and deer browsing. All field work was conducted with an approved study plan and memoranda of understanding between participating landowners. Within each deer density treatment, we randomly placed three, 30 × 5 m parallel belt transects spaced at least 30 m away from one another. Within each transect, we identified and measured the diameter at breast height (DBH) of all trees >5 cm DBH. From DBH, basal area was calculated at the transect level (150 m²) and then extrapolated to a per hectare basis (10,000 m²). Shannon diversity was calculated with basal area as the unit of abundance using R package VEGAN (Oksanen et al., 2020).

Canopy structural complexity was measured using a ground-based portable canopy LiDAR system (PCL; Parker et al., 2004). The PCL measures the arrangement of leaves and branches within a canopy using an upward-facing infrared laser at 2,000 Hz and is an economical means to rapidly collect and calculate multiple, high-resolution canopy structural metrics at the stand

scale. Canopy structural metrics were calculated using the FORESTR R package (Atkins, Bohrer, et al., 2018). Although FORESTR can calculate nearly two dozen canopy structural parameters, we focused on metrics that characterize four different aspects of canopy structural complexity and are commonly studied in relation to disturbance; vegetation area index (VAI; the density of vegetation within the canopy, or the density of LiDAR returns within each 1 × 1 m column along PCL transect), mean outer canopy height (MOCH; average maximum return height of lasers along transect), gap fraction (the openness of the canopy, or the ratio of PCL sky hits to vegetation returns), and rugosity (canopy structural complexity, or the vertical and horizontal heterogeneity in leaf, branch and stem distributions; Atkins, Bohrer, et al., 2018; Atkins et al., 2020). These metrics correlate well with important ecophysiological responses including above-ground primary productivity (ANPP, Fotis et al., 2018; Hardiman, Gough, et al., 2013) and leaf traits (Fotis & Curtis, 2017), and can characterize habitat heterogeneity features that predict wildlife diversity (e.g. Ishii et al., 2004; avian diversity, Seavy et al., 2009; squirrel habitat, Fotis et al., 2020).

Canopy metrics				
Treatment	VAI (m ² /m ²)	MOCH (m)	Gap fraction (%)	Rugosity (m)
4 deer/km ²	7.53 ± 0.07a	13.68 ± 0.70	0.81 ± 0.23a	7.40 ± 0.80ab
8 deer/km ²	7.34 ± 0.18a	12.09 ± 0.46	0.90 ± 0.26a	5.85 ± 0.49b
15 deer/km ²	7.62 ± 0.12a	12.32 ± 0.64	0.65 ± 0.22a	9.01 ± 0.70a
25 deer/km ²	6.17 ± 0.25b	14.96 ± 1.15	4.70 ± 1.35b	8.72 ± 0.92a
Effect	F3,17.2 = 9.45; p = 0.0007	F3,3.2 = 3.97; p = 0.0505	F3,39.6 = 8.02; p = 0.0003	F3,18.3 = 7.98; p = 0.0013

Stand metrics				
Treatment	Richness (S)	Stem density (N/ha)	Basal area (m ² /ha)	Diversity (H')
4 deer/km ²	4.67 ± 0.22	2,487 ± 191a	36.14 ± 1.89a	1.17 ± 0.14a
8 deer/km ²	5.25 ± 0.29	2,210 ± 106ab	27.64 ± 1.89bc	1.25 ± 0.14a
15 deer/km ²	4.56 ± 0.63	2,550 ± 178a	34.94 ± 2.27ab	0.91 ± 0.15ab
25 deer/km ²	3.92 ± 0.60	1,721 ± 191b	25.78 ± 1.89c	0.73 ± 0.14b
Effect	F3,16.7 = 1.51; p = 0.2474	F3,18.1 = 3.80; p = 0.0284	F3,39.4 = 6.44; p = 0.001	F3,38.4 = 6.43; p = 0.0012

Table 1. (top) Canopy complexity metrics (VAI, Mean Outer Canopy Height, Gap Fraction, Rugosity). (bottom) Stand metrics (Species Richness, Stem Density, Basal Area, Shannon Diversity) of trees as measured in 2016 within the clearcut sections of deer density treatments on the Allegheny Plateau

2.3 STATISTICAL ANALYSIS

We used analysis of variance (ANOVA) to assess treatment effects on stand structural attributes, species diversity, and canopy structural metrics using general linear mixed models (Proc GLIMMIX; SAS 9.4, SAS Institute, Inc.). Our experiment is a nested randomized complete block design where deer density is considered a fixed effect and both site and transect are considered random effects. This design assumes independent transects nested within each deer density treatment. This is modelled on Nuttle and colleague's (2014) approach within the same experiment and is reasonable given that tree basal area was low and distance between transects (≥ 30 m) was large, which likely exceeds direct canopy interaction distance between each transect (Lorimer, 1983). We tested this assumption by running exploratory analyses that modeled spatial autocorrelation among transects using a second, spatial power random effect. These models either had poorer

fit (i.e. higher AICc) or failed to converge, and did not change interpretation, suggesting spatial autocorrelation was minimal (See Appendix Tables S1 and S2¹). Nevertheless, we present those results so the reader can draw their own conclusions about potential spatial dependence.

Normality was tested using the Shapiro–Wilk test. Vegetation area index, rugosity, basal area, and tree species diversity (H') were normally distributed. Gap fraction, MOCH, DBH, species richness, and stem density were right-skewed. For these, continuous response variables were modeled using a gamma distribution, whereas count data used Poisson (richness) or negative binomial distribution (stem density). We graphically examined the normality of the residuals, tested the homogeneity of the variance using boxplots and Levene's tests. Where necessary, this residual variance was adjusted using a second random statement with a 'group=' option. All models used a Kenward–Roger denominator

¹ <https://doi.org/10.1111/1365-2664.14095>

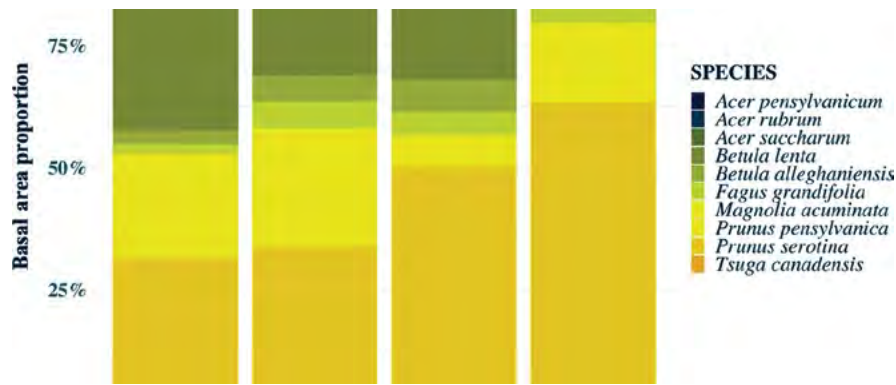


Figure 3. Proportional breakdown of species by basal area within each deer density treatment. As deer densities increase, so does the canopy dominance of unpalatable black cherry *Prunus serotina* (orange), while more shade-tolerant species decrease

degrees of freedom adjustment method. Where a significant (critical value = 0.05) deer density treatment effect was detected, we tested pairwise differences among deer density treatments with the LSMEANS function statement and used the Tukey–Kramer adjustment for multiple comparisons (Lenth, 2016).

3. RESULTS

3.1 STAND DIVERSITY, COMPOSITION AND STRUCTURE

We found a significant decrease in the Shannon diversity of tree species with increased deer density ($p = 0.001$, $F = 6.43$, Table 1 previous page) nearly 36 years after the initiation of the enclosure experiment, wherein the highest deer density treatments (15 and 25 deer/km²) were relatively depauperate and dominated by black cherry *Prunus serotina*. The lowest deer density

treatments had greater representation of pin cherry *Prunus pensylvanica*, red maple *Acer rubrum*, and birch *Betula* spp. as well as black cherry (Figure 3; Table 2). Across deer density treatments, black cherry's proportional abundance steadily increased with greater deer browse pressure (4 deer/ km² = 15.6%, 8 deer/km² = 18.4%, 15 deer/ km² = 39.5%, 25 deer/ km² = 60.4%), being the highest at the 25 deer/km², whereas the proportional abundance of all other species generally decreased (Table 2). While average species richness was also low at the 15 and 25 deer/km² treatment, there were no significant differences in richness among density treatments ($p = 0.25$, $F = 1.51$, Table 1; see also Tilghman, 1989). Stem density and basal area also decreased at the highest deer density. Stem density was highest at 4 and 15 deer/ km², had a moderate decrease

Table 2. Tree species density and proportional abundance by deer density treatment (APCE = *Acer pensylvanicum*; ACRU = *Acer rubrum*; BELEN = *Betula lenta*; BETAL = *Betula alleghaniensis*; FAGR = *Fagus grandifolia*; MAGAC = *Magnolia acuminata*; PRPN = *Prunus pensylvanica*; PRSR = *Prunus serotina*). Species that did not appear in more than two density treatments (*Tsuga canadensis* and *Acer saccharum*) were not included

Treatment	Species density (N/ha)								Total
	ACPE	ACRU	BELEN	BETAL	FAGR	MAGAC	PRPN	PRSR	
4 deer/ km ²	17 (0.7%)	211 (8.5%)	1006 (40.5%)	94 (3.8%)	172 (6.9%)	22 (0.9%)	567 (22.8%)	389 (15.6%)	2,487
8 deer/ km ²	6 (0.3%)	394 (17.8%)	489 (22.1%)	100 (4.5%)	344 (15.6%)	11 (0.5%)	461 (20.9%)	406 (18.4%)	2,210
15 deer/ km ²	15 (0.6%)	163 (6.4%)	652 (25.6%)	141 (5.5%)	400 (15.7%)	7 (0.3%)	89 (3.5%)	1007 (39.5%)	2,550
25 deer/ km ²	17 (1.0%)	61 (3.5%)	133 (7.7%)	78 (4.5%)	178 (10.3%)	0	217 (12.6%)	1039 (60.4%)	1,721

at 8 deer/km² and then was significantly lower than every other treatment at 25 deer/km² ($p = 0.03$, $F = 3.80$, Table 1). Basal area was highest at 4 deer/km² and 15 deer/km², moderately lower at 8 deer/km², and lowest at 25 deer/km² ($p = 0.001$, $F = 6.44$, Table 1). Both metrics varied with intermediate deer browsing but were consistently the lowest within the 25 deer/km² treatment.

3.2 CANOPY STRUCTURE

The highest deer density treatment also had significant effects on canopy complexity. Stands established at the highest browsing levels showed the lowest VAI ($p < 0.001$, $F = 9.45$, Table 1). There were no significant differences in VAI between the 4, 8 or 15 deer/km² stands. There was a concomitant increase in gap fraction for canopies in the 25 deer/km² treatment ($p < 0.001$, $F = 39.64$, Table 1), but little difference in this metric between the 4, 8 and 15 deer/km² treatments. Both VAI and gap fraction were strongly negatively correlated with one another and are treated as corresponding variables in the discussion ($r = -0.92$, Appendix Figure S1).

Rugosity, a measure of the heterogeneity in vertical and horizontal leaf, branch and stem distribution, showed substantial variation among deer density treatments. Rugosity was highest at 15 and 25 deer/km², lowest at 8 deer/km², and intermediate in the 4 deer/km² treatment ($p = 0.001$, $F = 7.98$, Table 1). Mean outer canopy height also varied among treatments, with trees in the 4 and 25 deer/km² treatments being an average of 1–3 m taller than trees in the 8 and 15 deer/km² treatments ($p = 0.051$, $F = 3.97$, Table 1).

4. DISCUSSION

The legacy of deer browse is still widely apparent in the experimental forest's species composition, stand structure, and canopy structural complexity, despite the deer density treatments having ended nearly three decades ago. As deer are present at high densities throughout

eastern North American forests, our results indicate that this severe press disturbance can have a dramatic influence on forest structure at multiple levels for many years.

High deer density at stand initiation led to low tree diversity in the overstorey, with black cherry being the dominant canopy species (Figure 3; Table 2). These results contribute to extensive literature showing that high deer browsing results in low plant diversity (Goetsch et al., 2011; Habeck & Schultz, 2015; Russell et al., 2017). Our observation that high deer densities favor black cherry growth is also supported by Royo et al. (2021) and by prior studies in stand development within our experiment (Horsley et al., 2003; Nuttle et al., 2011; Tilghman, 1989), further demonstrating the persistent legacy of deer browsing on stand diversity. Black cherry, being cyanogenic, is unpalatable to deer, making it one of the primary tree species to survive following the intense browse pressure in the 25 deer/km² treatment (Horsley et al., 2003). Other ecologically and economically valuable tree species, such as maple and birch, remain in low abundance in the 25 deer/km² treatments after 36 years (Figure 3).

High deer density treatments had low tree density and basal area as well, similar to the results of Horsley et al. (2003) who found that increasing deer density reduced stem density 5 years post-treatment. However, this browse effect on tree density was not observed by Nuttle et al. (2011) at 10- and 25-year post-treatment, who found little difference in tree density between treatments. They hypothesized that low-palatability species, such as black cherry, were able to regenerate and fill niche space of high-palatability species, consistent with Leibold's edibility hypothesis (Leibold, 1989; Nuttle et al., 2011). We suggest that over time, high deer densities at our site led to a recalcitrant understorey, with unpalatable hay-scented fern *Dennstaedtia punctilobula*

spreading during stand initiation and eventually dominating the understorey of most of the 25 deer/km² stands (Nuttle et al., 2014). As these stands began self-thinning, the fern understorey prevented tree regeneration through shading

and resource competition, as has been seen in other parts of Pennsylvania (Royo & Carson, 2006). The legacy effect of deer browse on tree density we observed has therefore likely re-emerged due to compositional differences in the regeneration layer among treatments, whereby a recalcitrant understorey prevented further tree regeneration following the self-thinning of uneaten, shade intolerant black cherry in high deer density areas. These results underscore the importance of long-term monitoring of stands afflicted by deer browse (or other press disturbance agents), as the effects of herbivory on stand structure may take decades to fully develop. Furthermore, these sparse black cherry stands at 25 deer/km² had the lowest basal area and thus, the lowest above-ground biomass, as both metrics are highly correlated ($r = 0.99$; Appendix Table S3). Low tree basal area at the highest deer density indicates that overabundant herbivore populations can cause reductions in above-ground carbon stocks over time through species community change (White, 2012).

The combination of changes in tree species composition and stand structure in the highest deer density treatment translated into changes in canopy structure: a stark decrease in VAI and increase in canopy gap fraction at 25 deer/km². Functionally, this implies a reduction in the density and connectivity of canopy leaves, with foliage now highly aggregated and clustered around black cherry stems (Figure 1). This finding aligns with Canham et al. (1994) who found that black cherry had the lowest crown depth (the proportion of tree height to tree-crown depth) of many common temperate tree species and Sullivan et al. (2017) who found that

shade intolerant species have narrower canopies. The deer browse effect on crown geometries and canopy structure, as quantified with the PCL, may also signal the beginning of a shift in forest structure to an alternative state, one described by Stromayer and Warren (1997) as a 'deer savanna'. In our system, high deer browse pressure caused significant changes in species composition, gap fraction, and VAI, with black cherry dominating the overstorey and hay-scented fern dominating the understorey.

The impact of deer on VAI presented herein is more similar to pulse disturbances, such as fire and ice storms, than press disturbances, such as acid rain or some pathogens. Deer, fire, and ice storms each reduce canopy VAI through species compositional changes, leaf combustion, or stem collapse, respectively (Atkins et al., 2020; Fahey et al., 2020). In contrast, acidification and pathogens such as hemlock woolly adelgid have shown relatively little influence on VAI, potentially because these slow-acting disturbances allow for foliar replacement in the canopy over time (Atkins et al., 2020). However, the impact of herbivory on canopy vegetative density is likely to be longer-lasting than a single fire or ice storm event. Deer have changed the stand's VAI through lasting shifts in species composition and canopy architecture rather than through moderate canopy combustion or breakage, which likely only have a short temporal signature. These long-term reductions in canopy density by deer can then influence ecological function, as VAI is strongly correlated with the fraction of photosynthetically active radiation (fPAR) absorbed by the canopy (Atkins et al., 2018) and influences wildlife such as arthropods, bird species, reptiles, and other arboreal species (Cuddington, 2011; Nuttle et al., 2011; Ulyshen, 2011).

Rugosity showed less straightforward treatment responses. The increase in rugosity associated with higher deer densities and gap fraction is similar to Fotis et al. (2018) who found that stands with low stem densities had more open canopies and greater horizontal variability, which contributes to greater rugosity. Since all of our stands are still in the stem exclusion phase, stands in the low deer density treatment are dense and less horizontally complex than stands in the high deer density treatment, causing a difference in rugosity. Our findings are consistent with the canopy structural classification system of Fahey et al. (2019), where dense forests in the stem exclusion phase have low rugosity and young, patchy canopies have slightly higher rugosity.

Other temperate forest disturbances have had variable influences on rugosity. Ice storms, hemlock wooly adelgid, and now white-tailed deer browse increase rugosity, age-related senescence decreases rugosity, while fires, historic logging, beech bark disease, and acidification have little effect (Atkins et al., 2020; Wales et al., 2020). The variable response of rugosity to disturbance type indicates that multiple canopy structural metrics should be considered to gain a more holistic perspective on which aspect(s) of the canopy change. As our stands continue to develop, rugosity could become a useful metric to predict NPP in light of herbivory disturbance, as it is strongly correlated with greater net primary productivity within maturing stands (Gough et al., 2019, 2021). Furthermore, since stand age and time since disturbance are of particular importance when measuring rugosity, but are often difficult to standardize across studies, long-term experimental studies such as ours are particularly important to better understand these disturbance–canopy interactions (Wales et al., 2020).

We found that tree canopies were tallest at the lowest (4 deer/ km²) and highest (25 deer/km²)

deer density treatments. This pattern may have been driven by differences in preferred browse species at each end of the deer density spectrum, with palatable pin cherry favored at 4 deer/ km² and unpalatable black cherry at 25 deer/ km² (Figure 3; Table 2). Both *Prunus* species are shade intolerant and fast growing, making the low and high deer density canopies taller than those dominated by more shade-tolerant species such as beech, maple and birch (Table 1; Figure 3; Canham et al., 1994). Differences in canopy height and composition could influence each stand's total above-ground biomass and ability to support various wildlife habitat types (Fotis et al., 2020; Seavy et al., 2009; Sullivan et al., 2017; Wang et al., 2021). These results support other studies showing that press disturbances can have a positive impact on MOCH through species-specific influences. For instance, soil acidification likely increases MOCH by favoring upper canopy growth and loss of subcanopy species (Atkins et al., 2020). Eichhorn et al. (2017) found that increased deer densities led to taller canopies in southern England, although the mechanism for this effect was unclear. Our experiment provides clear evidence that high deer densities impact canopy height decades after stand establishment by altering the relative abundance of tree species that vary in shade tolerance and growth rate. Such species-specific influences by press disturbances may be an important mechanism affecting changes in canopy height and structure.

Effective management of forest structure and canopy complexity in light of current or future disturbances is becoming a priority due to structure's many connections to ecosystem function and resilience (Fahey et al., 2018; Seidl et al., 2016). Using a PCL, we have gained insight on how a decade of deer browse disturbance can leave a distinct signal on the canopy, with high deer density leading to high rugosity, gap fraction, and canopy height, with low VAI. Since

ungulates are at high densities in many forests globally, our work provides a basis for generalizing how intense herbivory may affect key canopy structural traits over time (Bernes et al., 2018). By allowing ungulate populations to remain at high densities, forest managers are indirectly changing stand and canopy structure, which likely has important long-term ramifications on many associated ecosystem functions. Therefore, long-term monitoring of canopy structure in forests with heavily managed ungulate populations could serve as an indicator of both ecological function and management success (Gatica-Saavedra et al., 2017).

5. CONCLUSIONS

Using a long-term deer enclosure experiment, our study is the first to apply a PCL system to determine how varying deer densities affect canopy structure. We show that deer leave a unique legacy on the structure of northern hardwood forests at multiple levels, from species diversity to canopy complexity, and that these changes can be detected with the PCL. Over three decades after the conclusion of the experimental treatments, at the highest deer density treatment we saw decreases in tree diversity, basal area, tree density, canopy VAI, and increases in gap fraction and rugosity. Furthermore, we found that tree density and basal area varied widely with different deer browse intensities due to changes in species composition and that these effects of deer browse may take decades to become fully pronounced. Although the influence of herbivory is pervasive across many forest types (Bernes et al., 2018; Patton et al., 2018), there has been little prior quantitative evidence of the legacy of browsing pressure on canopy structure in temperate forests. Deer herbivory may be one of the most important drivers of forest composition and canopy structure over long time-scales, which could have significant

ramifications on wildlife habitat (Fotis et al., 2020), carbon sequestration and storage (Fotis et al., 2018; Gough et al., 2020; Hardiman et al., 2011), light-use efficiency (Atkins, Fahey, et al., 2018; Hardiman, Gough, et al., 2013), and timber extraction (Miller et al., 2009) in the present and into the future. 🌲

Samuel P. Reed is with the Department of Forest Resources at the University of Minnesota, St. Paul, Minnesota

Alejandro A. Royo is with the Forestry Sciences Lab, USDA Forest Service, Northern Research Station, Irvine, Pennsylvania

Alexander T. Fotis, Kathleen S. Knight, Charles E. Flower are with the USDA Forest Service, Northern Research Station, Delaware, Ohio

Peter S. Curtis is Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio

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Editor's Note

Threats to and Viability of Missouri's Natural Areas

In recent years, the concept of maintaining ecosystem resilience in an altered natural world has taken on greater significance in light of rapid environmental change. Efforts to improve biodiversity resilience in natural communities surrounded by urban and agricultural development and the ensuing disruption of ecological processes requires thoughtful, careful planning and implementation. One of the core concepts of resiliency of natural spaces involves size; larger natural zones tend to allow for greater ecosystem function (Biller, et al. 2009).

For the past 25 years or more, the Missouri Natural Areas Committee has embraced the concept that resilient ecosystems often require large-scale zones with buffer areas of similar landscape types. In recent years, for example, following a long history of restoration, the committee approved the expansion of the Coakley Hollow Fen NA from 5 acres to 1,773 acres to include the surrounding diverse woodlands and fens. Small, though intact high quality natural communities including small patches of railroad remnant prairies or sinkhole ponds, have great value in protecting and preserving biodiversity. However, they come with their own significant external threats. In the case of the railroad remnant prairies, one fast swipe of roadside herbicide can cause them to wink out forever.



Image 1. Lincoln Hills Natural Area (1,872 acres) in Cave River State Park (MDC, 4,400 ac.) encompasses a smaller natural area, Pickensville Pond, a small sinkhole pond natural area designated in the 1980s. The natural area surrounding Pickensville Pond expanded in 1988 to include the frequently burned and managed surrounding woodlands. Deer and exotic species management have occurred in the natural area and throughout the park for over 35 years. Urban encroachment at the park borders remains a viable threat, and staff work annually to continue management of this landscape scale natural area.

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