## Conservation Issues

## Primeval Paths: Bison in West Virginia

Melissa A. Thomas-Van Gundy, 1,6 Jessica D. Perkins, 2 Crystal Krause, 3 Cynthia D. Huebner, 4 Lorenzo Ferrari, 4 and Linda S. Smith 5

<sup>1</sup>USDA Forest Service, Northern Research Station, Parsons, WV

<sup>6</sup>Corresponding author: melissa.thomasvangundy@usda.gov; 304-478-2000

Associate Editor: Scott Schuette

#### **ABSTRACT**

Approximately 2600 km of bison and elk trails have been mapped in West Virginia using historical records, including county histories and travelers' accounts with published dates between 1876 and 1977. Most points of interest associated with these trails document European bison or elk hunting events. We explore some potential uses of the digital trails data and discuss the limitations of the data and need for further refinements. This map of major bison trails (available for download at https://doi.org/10.2737/RDS-2021-0055) is an important resource for telling a more complete story of the history of forests and woodlands of West Virginia.

#### INTRODUCTION

The bison (Bison bison L.) is an iconic symbol of the Americas, symbolized on United States coinage and named the National Mammal of the United States of America in 2016 (Pub. L. 114-152). Although smaller in size compared to its Pleistocene counterparts (Shapiro et al. 2004; Hill et al. 2008), it is one of the last surviving members of megafauna on the continent, most of which perished during the late Quaternary extinction event (Koch and Barnosky 2006; Meltzer 2020). Its historical range spans large portions of North America, including the far eastern United States (Meagher 1986). In West Virginia, the last known bison, a cow and a calf, were killed in Randolph County near the town of Valley Head in 1825 (Maxwell 1898). The historical account details that the pair were spotted in Webster Springs (Webster County) and tracked across Gauley Mountain into the watershed of the Tygart Valley River. In this valley, bison and Native American trails connect north to south and east to west. The Seneca Trail or Warrior Path, also known as the Shawnee Trail, runs through Tygart Valley, mostly as U.S. Route 219. Along that route is a historical marker noting the deaths of the last bison in the state.

In 1989, one of the authors (L.S. Smith) was contracted by the Natural Heritage Program of the West Virginia Division of Natural Resources (WVDNR) to research old travelers' accounts and other records to document bison trails in West Virginia. Also included in this effort were the locations of springs and wallows used by bison and all other mentions of bison and use of the trails, springs, and wallows by elk (*Cervus canadensis* Erxleben). This work was undertaken because of the rediscovery of a rare plant considered extirpated from West Virginia, the running buffalo clover (*Trifolium stoloniferum* Muhl. ex A. Eaton). The clover, thought to be associated with bison trails

(Bartgis 1985; Campbell et al 1988), is on the Federal endangered species list and is currently (in 2021) proposed for removal from the list. The map was used to focus field surveys for locating clover populations. Although never published, this work has been used by land managers in the WVDNR and the Monongahela National Forest for years, with older employees passing on paper copies of the map to newer employees.

Although considered an animal of the western United States plains (Freese et al. 2007), bison were also present in the eastern United States from Pennsylvania southward to Georgia and Mississippi. Many geographers have considered the bison a recent addition to the woodlands of eastern forests; however, more current research with updated dating techniques sheds new light on this assumption. Like the accounts in West Virginia, the idea that bison only recently inhabited Illinois was based on the mismatch between early European accounts of abundant bison versus lack of bison remains at archaeological sites. A review of bison remains at both paleontological and archaeological sites across Illinois, 133 total, found that bison appeared in the area in the early Holocene (about 8000 y before present), with their numbers increasing after 4000 y before present and dramatically increasing after the 1500s (McMillan 2006). The Allegheny Mountains were generally considered the eastern boundary of the bison range, but evidence exists that some bison were present east of the Alleghenies in Virginia at the time of early European settlement (McWhorter 1915). In fact, the first written documentation of bison by European explorers was near what is now Washington D.C. (Hornaday 1889).

Salt springs are a possible habitat feature of eastern deciduous forests used by bison (Jakle 1968, 1969). However, without adequate food, bison would not have been able to travel hundreds of miles for salt. Consequently, networks of meadows, glades, barrens, savannas, open woodlands, and other grassland

<sup>&</sup>lt;sup>2</sup>West Virginia Division of Natural Resources, Elkins, WV

<sup>&</sup>lt;sup>3</sup>Davis and Elkins College, Elkins, WV

<sup>&</sup>lt;sup>4</sup>USDA Forest Service, Northern Research Station, Morgantown, WV

<sup>&</sup>lt;sup>5</sup>Retired USDI Fish and Wildlife Service, Brownsburg, VA

features must have been present in sufficient numbers to provide bison with adequate forage and wallow areas. Salt springs funneled herds into specific sites, thus creating major trails that were part of an intricate network of branching pathways.

Through this article we will document the development of the map of major bison trails and points of interest regarding bison and elk in West Virginia. We also investigate possible research applications of the map including exploratory analysis of the distance from a bison trail to current locations of rare plants in West Virginia including running buffalo clover. We also explore the possibility of human use of the bison trails in an analysis of the concentration of pyrophilic (fire-adapted) tree species and distance to a bison trail.

#### **METHODS**

#### Study Area

Elevational gradients explain much of the variation in the distribution of plants and animals in West Virginia, nicknamed "The Mountain State," with the lowest elevation in the state found on the Potomac River at about 73 m and the highest at Spruce Knob at 1482 m. The Eastern Continental Divide along the Allegheny Mountains within West Virginia creates a rain shadow effect on the eastern side of the mountain range that also strongly influences the plant and animal distributions.

To better capture this variation, managers in the WVDNR modified the West Virginia Ecoregions defined by USDA Forest Service at the Section level (Keys et al. 1995) into four regions based on geology, physiography, climate, hydrology, vegetation, and soils. The four modified ecoregions are the Allegheny Mountains, Cumberland Mountains, Ridge and Valley, and Western Allegheny Plateau (Figure 1). The descriptions that follow are adapted from the 2015 West Virginia State Wildlife Action Plan (WVDNR 2015).

Moving roughly from east to west across the state, the Ridge and Valley Section ( $\sim$ 14% of the state) is composed of folded and faulted layers of sedimentary rock, mostly sandstones and shales, and outcrops of limestone and dolomite. In this ecoregion is the lowest elevation point in the state, but the area also contains the greatest range of elevation with some ridges exceeding 1200 m. This ecoregion lies east of the rain shadow of the Allegheny Mountains and is relatively dry although climate varies with elevation within the region. The wide valley bottoms of this ecoregion have a long history of human settlement and conversion to agriculture. Due to its relative dryness, fire was historically more important here helping maintain open oakpine woodlands (Thomas-Van Gundy and Nowacki 2013).

The highest elevations in the state are found in the Allegheny Mountains Section (~25% of the state). Due to the high elevational setting, this region receives the highest rainfall and has the coldest temperatures and shortest growing season in the state. This region is distinct from the Ridge and Valley in that the geology is no longer defined by folding and faulting. Instead the sedimentary rocks, mostly sandstones and shales again, are in gently tilted formations. Significant outcrops of limestone are found in the region forming caves and higher pH soils in contrast to the mainly acidic soils formed from the sandstones and shales. The Eastern Continental Divide is the eastern edge of

this ecoregion; water on the west side drains to the Ohio River while water on the east drains to the Potomac River and eventually into the Chesapeake Bay.

Comprising  $\sim$ 22% of the state, the Cumberland Mountains Section has a climate that is uniformly warm and moist, with small-scale differences related to slope position and aspect. The area is a highly dissected plateau of narrow valleys and low mountains with steep slopes and narrow ridges and, in some places, deep gorges cut into nearly flat plateaus. Sandstones and shales again dominate the geology with formations in nearly level layers with extensive coal seams.

The Western Allegheny Plateau (~38% of the state) ranges from the foothills of the Allegheny Mountains west to the Ohio River and includes the entire Northern Panhandle. This Section has the lowest mean elevation and lowest elevational range in the state. Like the Cumberland Mountains, the climate is uniformly warm and moist with slight temperate and moisture variation from far west to far north. Nearly level layers of sedimentary rock, mainly sandstones and shales, form a landscape of a highly dissected plateau of low hills. Currently, there are population centers scattered throughout river valleys in this Section, and it has the highest human population in the state. There is abundant evidence of prehistorical human occupation as well.

#### Development of Original Map

County histories and journals of early explorers of what is now West Virginia were reviewed in 1989 for mention of game trails and general descriptions of wildlife and flora. The libraries and collections of Davis and Elkins College, Elkins, West Virginia (West Virginia Collection and Archives), West Virginia University, Morgantown, West Virginia (West Virginia Collections, Forestry Library, Wise Library, Evansdale Library, and Health and Science Library), Marshall University, Huntington, West Virginia (Special Collections and Morrow Library), and the West Virginia Department of Culture and History, Cultural Center, Charleston, West Virginia, were included in the search for documents. Key words such as clover, fields, meadows, grass, and direct mentions of bison/buffalo, elk, or general game or "Indian" trails were searched for and noted.

These trails and points were hand-drawn onto USGS quadrangle maps (1:62,500) for the state and deposited with the WVDNR for use and storage. The lines and points on the quadrangle maps were consolidated onto 1:500,000 maps of the state and shared with land management partners, such as the USDA Forest Service, along with the original report (Supplemental Appendix 1).

## **Updates to Original Map**

At the request of the now retired WVDNR Botanist, WVDNR GIS and Technical Support staff undertook an effort to digitize historical bison trails and points of interest for future use. Staff duplicated earlier mapping efforts by heads-up digitizing over 1:24,000-scale topographic (pre-1992 7.5-minute quadrangle) basemaps within ArcMap. Locations, points, and trail lines were located in ArcMap at the more detailed scale, using the descriptions and paper 1:62,500 maps. Points and lines were digitized over the identified location on the 1:24,000-scale basemap, following features on the new maps used as references

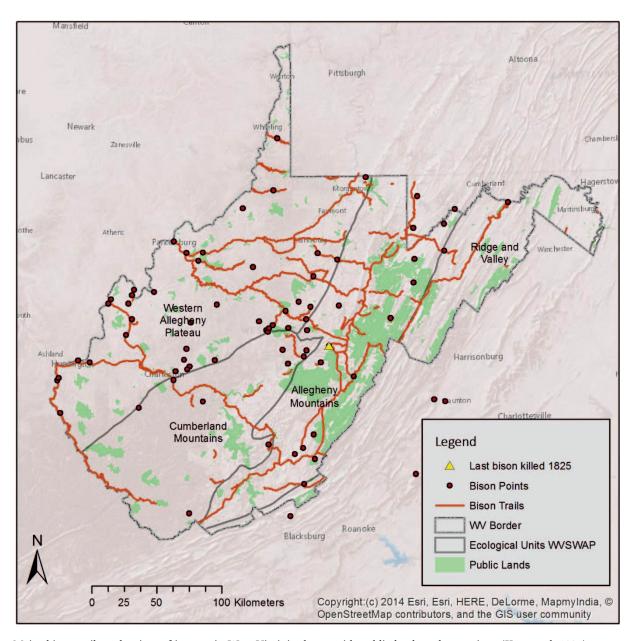


Figure 1.—Major bison trails and points of interest in West Virginia shown with public lands and ecoregions (Keys et al. 1995).

on the old maps. Staff used additional GIS basemap data to check the accuracy of locations based on the description.

# Relationship between Running Buffalo Clover and the Mapped Bison Trails

The original map was used to help focus survey efforts for the endangered running buffalo clover. Currently, WVDNR and Davis and Elkins College researchers are using the updated digital version of the bison trails in models to define habitat for running buffalo clover. These exploratory models include distance to bison trail as an input variable. The goals of this modeling project were to help identify search areas of high-quality habitat, gain insight on the physical requirements of the species, and guide conservation planning. Occurrence data for running buffalo clover were collected from Natural Heritage Programs across the species' range and environmental variables

were assembled to represent the physical environment including climate, geology, solar radiation, terrestrial habitat, distance to roads, distance to bison trail, and distance to urban centers. Running buffalo clover occurrence data included in the models were reviewed by WVDNR biologists to only include current and spatially accurate populations.

Models were developed for running buffalo clover in West Virginia at 30 m resolution and each scenario is a combination of bioclimatic, vegetation, geologic, and landscape variables. Variable selection was completed through consultation of a species expert and a sample spatial analysis to help identify variables with biological importance. Using known locations of running buffalo clover, three different models were developed from these variables to remove correlation and identify variables important to the presence of running buffalo clover. Scenario 1 included three climate variables, all terrestrial habitat variables,

Ecoregion	Area (km²)	Bison point count	Percentage of points	Trail length (km)	Percentage of length	Density of trails (km/km²)
Allegheny Mountain	16,110.9	14	19	944.6	34.9	0.059
Cumberland Mountain	13,773.0	10	13	318.6	11.8	0.023
Ridge and Valley	8499.1	3	4	224.3	8.3	0.026
Western Allegheny Plateau	24,272.8	40	53	1151.1	42.6	0.047
WV Total	62,655.8	67	89	2638.7	97.6	
Total		75		2703.4		

**Table 1.—**Bison point counts and trail lengths and density by Ecological Section.

all geologic variables, and all landscape variables. Scenario 2 included the same three climate variables as scenario 1, all terrestrial habitat variables, no geologic variables, and all landscape variables. Scenario 3 included additional climate variables to include precipitation, solar radiation, all terrestrial habitat variables, all geologic variables, and all landscape variables. The three scenarios were analyzed and compared using MaxEnt modeling methods and validated by jackknife analysis by known species location.

This work is part of an ongoing project in that includes modeling habitats for all listed plants of West Virginia with MaxEnt and comparing those results with the Random Forest models produced in Virginia in collaboration with NatureServe. An important factor for choosing MaxEnt was that it allows for the use of presence-only species data, and continuous and categorical environmental variables.

## Possible Correlations between the Occurrence of WV Plant Species of Concern and the Bison Trails

Other plant species considered rare in West Virginia (ranking of S1, S2, or S3) may be associated with disturbance caused by bison travel in the state from large river valleys (i.e., Ohio River) to uplands (Allegheny Mountains). For exploratory purposes, the West Virginia Natural Heritage Program database was queried for locations of all terrestrial vascular plants considered rare in the state (WVDNR 2020). For this exercise, we used all vascular plant element occurrences and did not exclude sites based on any precision threshold. The species were categorized by habitat type in one of four broad categories: woodland/ meadow/open, rock/cliff, wetland/riparian, or mature forest. The categories were based on the authors' knowledge of terrestrial habitats in the state and category assignments made through referencing regional and state floras and other available literature (Supplemental Appendix 2). The mean distances to these species' occurrence locations from a bison trail were calculated to determine if any broad trends were evident that might be useful in developing habitat models for these plants. The mean distances were summarized by 500 m groupings for display of trends by habitat group. Given the variety in habitat types and plants, many plants were assigned to multiple habitat types.

#### Comparison of Bison Trails with Pyrophilic Tree Species

The map of main bison trails may be used to explore the influence of bison and anthropogenic fire on the forests of West Virginia. Trees listed in surveys and deeds for the area within the proclamation boundary of the Monongahela National Forest were classified as either pyrophilic or pyrophobic and the percentage of pyrophilic trees calculated and interpolated

between deed corners (Thomas-Van Gundy and Nowacki 2013). As an example for a use of the digital trail map, we buffered the bison trails by 500 m and the area in pyrophilic percentage clipped to this buffer and summarized by percentage of the total area by pyrophilic classes (10% categories).

#### RESULTS AND DISCUSSION

The 1989 search of historical documents resulted in mapping 2639 km of trails in West Virginia either described as general game trails, trails specific to bison, or combination bison and Native American. The greatest length of trails is found in the Western Allegheny Plateau section (1151 km) and the largest number of points of interest (40) are found here as well, as might be expected given the movement of bison from Ohio and Kentucky into West Virginia and the predominance of this ecoregion in the state (Table 1). As described in the original report, the highest density of trails is found in the Allegheny Mountains section at 0.06 km of trail per square kilometer of land with trail density in the Western Allegheny Plateau only slightly lower at 0.05 km/km<sup>2</sup>.

The entire state was crisscrossed with bison trails when the first European settlers arrived. Some of these trails were still visible 100 y after the last bison was found in the area. Several trails branched out east from Wood County with one following the Little Kanawha River over to the Tygart Valley where numerous trails came together, a dense concentration of trails greater than any other place in the state. The old fields of the South Branch Valley in the eastern panhandle attracted the herds east from there, creating the trail later known as the McCullogh Trail, a frontier trail used by early explorers and settlers. This trail and others provided Trans-Allegheny access from the east and were well engineered, following the most direct route over the easiest grades and oftentimes along ridgetops. Many of the former bison trails were followed, at least in part, by later road and railroad construction. The Baltimore and Ohio Southwestern Railroad from the Potomac River to Parkersburg is a good example. The old Midland Trail, also known as U.S. Route 60 from White Sulphur Springs and Lewisburg west through Teays Valley, was one of the most famous bison trails in the state. In a sense, we are still following primeval pathways.

The classification of the point data on the map (Table 2) shows an emphasis on European hunting activities with 27 hunting mentions out of 81 activities or points of interest. Bison mentions were greater than elk with a total of 52 compared to 10, with both animals associated with 14 points. Surprisingly, only two wallows were mentioned and 12 meadows or fields.

**Table 2.**—Classification of the 75 points of interest from the 1989 report by type; note a point may be classed as having more than one type of information.

	Animal				
Point type	Bison	Elk	Both	None	Total
Native American hunting	3				3
European hunting	17	8	2		27
Field/meadow	6		3	3	12
Place name	5	2	1		8
Salt lick	12		6		18
Animal sighting	4		1		5
Trail crossing	4		1	1	6
Wallow	1			1	2
Total	52	10	14	5	81

## Running Buffalo Clover and Bison Trails

These results are preliminary and exploratory and presented here simply as examples of the potential for the bison trail map to be used to answer various landscape-scale questions.

Distance to bison trail was not an important variable for any of the models created for the occurrence of running buffalo clover, however of the 687 occurrence points in the model, 174 were within 2500 m Euclidian distance from a trail. For scenarios 1 and 3, the top five contributing variables were geological with the presence of Greenbrier Group geology contributing 42.9% to the determination of suitable running buffalo clover habitat in Scenario 1 and 45.6% in Scenario 3. Under Scenario 2, distance to road was found to be the most important variable, contributing 37.2% to the determination of running buffalo clover habitat. However, the response curve indicates higher suitability for running buffalo clover is found with decreasing distance to a bison trail (Figure 2). Interestingly, the location of the first herbarium sample of running buffalo clover in the state, collected in 1940 and site location reestablished in 1982, is about 2500 m from the bison trail between the towns of Webster Springs and Centralia.

**Table 3.**—Mean distance of state rare plants to a bison trail. Note: many plants were assigned to more than one habitat type.

Rare plant species group	Mean distance to trail (m)			
All species	8302			
Woodland/meadow/open	7835			
Rock/cliff	7378			
Wetland/riparian	8391			
Mature forest	9351			

## Other WV Rare Species and Bison Trails

There are 436 vascular, nonaquatic, rare plant species known and tracked in West Virginia. Of those, we categorized 278 or about 63% as having woodland/meadow/open habitat, 128 (29%) as rock/cliff, 229 (52%) as wetland/riparian, and 135 (31%) as mature forest. Since plants were classified in more than one habitat type, percentages sum to greater than 100. The mean distance to a bison trail for all rare plant species is about 8300 m (Table 3). The mean distance for rare plants associated with rock/cliff and woodland/meadow/open habitats is lower than all species combined at about 7380 m for rock/cliff and 7830 m for woodland/meadow/open habits (Table 3). As displayed by frequency of species element occurrences by distance bins of 500 m, the differences between habitat groups is more apparent (Figure 3). While this rough analysis is not proof of rare plant association with bison trails, this does support the need for quality woodland, field, and meadow habitat in the state. Given that many bison trails are now roads, and towns like Webster Springs were developed on known bison water sources, the lack of direct correlation of rare plants to bison trails is not surprising. Future research would include increasing the number of habitats into narrower categories, removing species that occur in multiple habitat types, or removal of some of the vascular plant data based on locational uncertainty or representation accuracy.

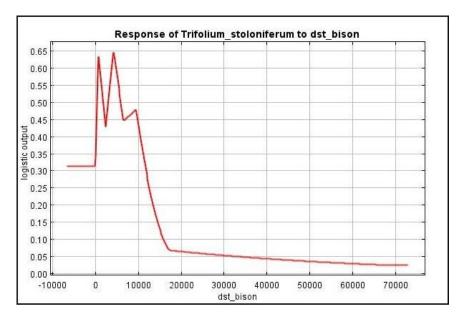


Figure 2.—Response curve for running buffalo clover suitable habitat and distance (m) to a bison trail.

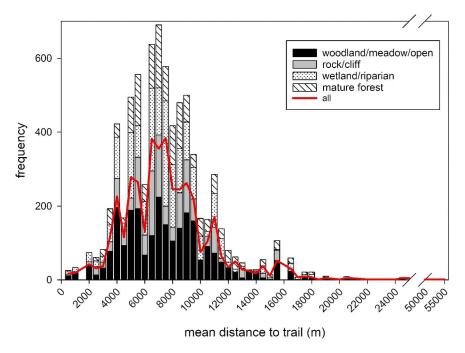
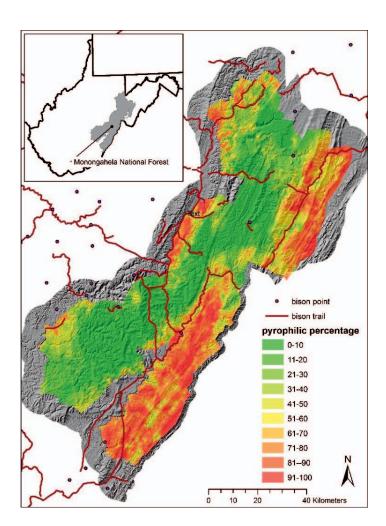


Figure 3.—Mean distance to a bison trail (by 500 m distance bins) for rare plant species element occurrences by habitat group. Note: many plants were assigned to more than one habitat type (Supplemental Appendix 1).



## Pyrophilic Tree Species and Bison Trails

The possible influence Native American use of the bison trails on the fire-adapted trees on the forest of what is now the Monongahela National Forest appears possible when the trails are overlaid on the map of fire-adapted tree species at European settlement (Figure 4). However, when the area (all ownership, not just national forest system lands) within a 500 m buffer of the trails is plotted by percent pyrophilic class, the influence appears less straightforward (Figure 5). About 14% of the area is in the 61–70% pyrophilic percentage class. The area in pyrophilic percentage above 60% is about 41% of the area and about 53% of the area is in pyrophilic classes above 50%. An important consideration missing from this initial analysis is the possible association of both rare plants and fire-adapted trees to landscape features the trails lead to and not necessarily the trails themselves.

## Limitations and Future Research Needs

As stated in the original documentation, this is a map of estimated routes. The accuracy of the travelers' accounts is hard to quantify now with the resulting land-use change and loss of visible evidence of the trails. Given that they are described in the original report as the main bison and elk trails in West Virginia, we can assume many minor trails are missing.

The conversion of the quadrangle maps and points to digital versions gives the illusion of a level of precision and accuracy that is likely impossible to quantify. We caution users of the trail

**Figure 4.**—Bison trails and the pyrophilic (fire-adapted) trees of the area within the proclamation boundary of the Monongahela National Forest. Pyrophilic map based on analysis of witness trees in deeds and surveys from 1752 to 1899 (Thomas-Van Gundy and Nowacki 2013).

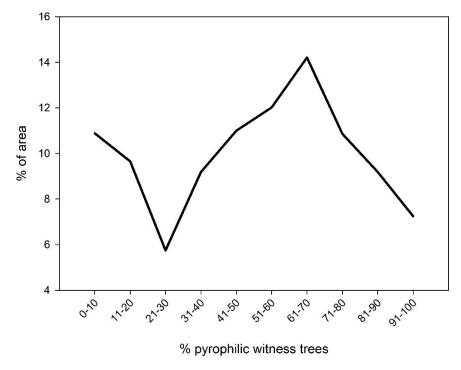


Figure 5.—Percent of area within 500 m of a bison trail by pyrophilic percentage class from within the proclamation boundary of the Monongahela National Forest (includes public and private ownership).

map that at some scale, depending on the questions being asked, the location of these lines is not reliable. The original trails were hand-drawn onto 1:62,500-scale topographic maps and every effort was made to duplicate lines accurately at the more detailed 1:24,000-scale but inherent errors may exist.

With many libraries and collections available in digital format, this work would no doubt benefit from cooperation with a historian to determine if more sources of information are now available. The current map includes points and trail segments that reach into adjacent states, which could be expanded upon with further review of the literature. The points of interest and locations of rare plants in woodland or meadow habitats could be used to connect trail segments. Other sources of information, such as the locations of salt and freshwater springs, could also be used to connect the main trails or hypothesize the locations of minor trails. Location data for archaeological sites would also be useful in future analyses and future research would benefit from the inclusion of an archaeologist.

#### **CONCLUSIONS**

While considerable change has occurred in the forests of West Virginia (Thomas-Van Gundy and Morin 2021), this documented presence of a nomadic grazer in the state is useful for a complete picture of past conditions. These large animals would have directly altered the landscape through their creation of paths and their consumption of vegetation. Their presence would have been evidenced at bison wallows, and clay and salt deposits as well. The ties between Native Americans and bison are still being explored for West Virginia, especially in the highlands where less is known about Native American resource use. This map of major bison trails is an important resource for

telling a more complete story of the history of forests and woodlands of West Virginia.

#### **ACKNOWLEDGMENTS**

Throughout the years, many people have supported this work and recent support for the digital map came from P.J. Harmon, botanist with WVDNR (retired). We thank Chris George, WVDNR, for his work on the most recent digital version. We thank Greg Nowacki and Jason Stevens, USDA Forest Service, Eastern Region, and an anonymous reviewer for their helpful reviews of early drafts of this manuscript.

Melissa Thomas-Van Gundy is a research forester with the USDA Forest Service, Northern Research Station in Parsons, WV. Her research interests include stand- and landscape-level projects focused on restoration and sustainable management of forested ecosystems. She holds a PhD from West Virginia University.

Jessica Perkins is the Geographic Information Systems (GIS) & Technical Support Program Manager for West Virginia Division of Natural Resources, Wildlife Resources Section in Elkins, WV. She is a Certified GIS Professional with over 20 years of GIS management and analysis experience. She holds a Master of Forestry and Graduate Certificate in Geospatial Information Technology from Virginia Tech.

Crystal Krause is an associate professor with Davis & Elkins College in Elkins, WV. Her research interests include developing spatial models to help identify potential impacts of climate change on rare and endemic species. She holds a PhD from Northern Arizona University.

Cynthia D. Huebner is a research botanist with the USDA Forest Service, Northern Research Station in Morgantown, WV. Her research interests include invasive plant biology and ecology, their impacts on ecosystems (including rare plant communities), and their interactions with native plants (including plant species of concern). She holds a PhD in botany from Miami University of Ohio.

Lorenzo Ferrari is a botanist with the USDA Forest Service, Northern Research Station in Morgantown, WV. His research interests include invasive and native plant species biology and ecology in forested ecosystems. He holds a master's degree from Auburn University.

Linda S. Smith retired as a biologist from the USDI Fish and Wildlife Service.

#### LITERATURE CITED

- Bartgis, R.L. 1985. Rediscovery of *Trifolium stoloniferum* Muhl. ex. A. Eaton. Rhodora 87:425-429.
- Campbell, J.J.N., M. Evans, and M.E. Medley. 1988. Buffalo clovers in Kentucky (*Trifolium stoloniferum* and *T. reflexum*): Historical records, presettlement environment, rediscovery, endangered status, cultivation, and chromosome number. Rhodora 90:399-418.
- Freese, C.H., K.E. Aune, D.P. Boyd, J.N. Derr, S.C. Forrest, C.C. Gates, P.J. Gogan, S.M. Grassel, N.D. Halbert, K. Kunkel, and K.H. Redford. 2007. Second chance for the Plains bison. Biological Conservation 136:175-184.
- Hill M.E. Jr., M.G. Hill, and C.C. Widga. 2008. Late Quaternary bison diminution on the Great Plains of North America: Evaluating the role of human hunting versus climate change. Quaternary Science Reviews 27(17-18):1752-1771.
- Hornaday, W.T. 1889. The extermination of the American bison. Government Printing Office, Washington, D.C.
- Jakle, J.A. 1968. The American bison and the human occupance of the Ohio Valley. Proceedings of the American Philosophical Society 112:299-305.
- Jakle, J.A. 1969. Salt on the Ohio Valley frontier, 1770-1820. Annals of the Association of American Geographers 59:687-709.
- Keys, J. Jr., C. Carpenter, S. Hooks, F. Koenig, W.H. McNab, W. Russell, and M.L. Smith. 1995. Ecological units of the eastern United States First approximation (CD-ROM). U.S. Department of Agriculture, Forest Service, Atlanta, GA.
- Koch, P.L., and A.D. Barnosky. 2006. Late Quaternary extinctions: State of the debate. Annual Review of Ecology, Evolution, and Systematics 37:215-250.
- Maxwell, H. 1898. History of Randolph County. Acme Publishing Co., Morgantown, WV (reprinted in 1961, McClain Printing, Co., Parsons, WV).
- McMillan, R.B. 2006. Perspectives on the biogeography and archaeology of bison in Illinois. Pp. 67-147 *in* R.B. McMillan, ed., Records of early bison in Illinois. Illinois State Museum Scientific Papers 31, Springfield, IL.
- McWhorter, L.V. 1915. Border Settlers of Northwestern Virginia. Republican Publishing Co., Hamilton, OH.
- Meagher, M. 1986. Bison bison. Mammalian Species 266:1-8.
- Meltzer, D.J. 2020. Overkill, glacial history, and the extinction of North America's Ice Age megafauna. Proceedings of the National Academy of Sciences 117(46): 28555-28563.
- Shapiro B., A.J. Drummond, A. Rambaut, M.C. Wilson, P.E. Matheus, A.V. Sher, O.G. Pybus, M.T.P. Gilbert, I. Barnes, J. Binladen, et al.

- 2004. Rise and fall of the Beringian steppe bison. Science 306:1561-1565.
- Thomas-Van Gundy, M., and R. Morin. 2021. Change in montane forests of east-central West Virginia over 250 years. Forest Ecology and Management 479(1):118604.
- Thomas-Van Gundy, M.A., and G.J. Nowacki. 2013. The use of witness trees as pyro-indicators for mapping past fire conditions. Forest Ecology and Management 304:333-344.
- Thomas-Van Gundy, M.A., J.D. Perkins, and L. Smith. 2021. Primeval paths: Bison in West Virginia. USDA Forest Service Data Archive, Fort Collins, CO. <a href="https://doi.org/10.2737/RDS-2021-0055">https://doi.org/10.2737/RDS-2021-0055</a>
- [WVDNR] West Virginia Division of Natural Resources. 2015. State Wildlife Action Plan. <a href="https://www.wvdnr.gov/2015%20West%20Virginia%20State%20Wildlife%20Action%20Plan%20Submittal.pdf">https://www.wvdnr.gov/2015%20West%20Virginia%20State%20Wildlife%20Action%20Plan%20Submittal.pdf</a>
- [WVDNR] West Virginia Division of Natural Resources. 2020. Biotics database records of rare species and natural communities. West Virginia Natural Heritage Program, WVDNR, Elkins, WV. Queried on 30 Oct 2020.