Native and novel habitat assessment and impact of fire on yellow fumewort (*Corydalis flavula*)

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Cover: *Left* - yellow fumewort flowers and fruits; *Right* - yellow fumewort habitat with black locust (*Robinia pseudoacacia*) in background, and garlic mustard (*Alliaraia petiolata*) and sweet cicely (*Osmorhiza* sp.) dominant.

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Abstract

Yellow fumewort (*Corydalis flavula* (Raf.) DC., Papaveraceae) is listed as a threatened species in Michigan. While several historical occurrences of yellow fumewort occur within floodplain forests, the majority of extant occurrences are found in early-successional forests dominated by the invasive tree, black locust (*Robinia pseudoacacia*), centered within Fort Custer National Guard Training Center (FCTC) near Augusta, MI. Understanding how to manage these core populations of yellow fumewort is of vital importance for the persistence of the species in Michigan. I conducted surveys and plot sampling to better understand the management of yellow fumewort. First, I conducted surveys in portions of the Kalamazoo River floodplain near to know populations, to document new occurrences and to compare habitat between novel (black locust-dominated) and native (floodplain) habitats. These surveys were conducted at Fort Custer Recreation Area (FCRA) and the Southwest Michigan Land Conservancy's (SWMLC) Augusta Floodplain-Emmons Preserve. I observed no populations of yellow fumewort within the floodplain, although I did document new populations on slopes adjacent to the floodplain at FCRA, in areas dominated by black locust. Second, I established 0.1 ha monitoring plots to compare demographic responses of yellow fumewort to habitat differences and management with prescribed fire. Three plots each were established in areas near the Kalamazoo River within FCRA, areas slated for prescribed fire in spring 2021 at FCTC and the SWMLC Chipman Preserve, and control areas at FCTC and Chipman. At each plot, I collected data on trees, shrubs, ground cover (leaf litter, bare ground, etc.), ground layer species composition, and abundance of yellow fumewort. This report primarily serves to summarizes these findings and describe the methodology. Subsequent studies will track yellow fumewort in the 0.1 ha plots, and report on changes to demographic parameters in response to both habitat differences and application of prescribed fire.

Introduction

Yellow fumewort (*Corydalis flavula* (Raf.) DC., Papaveraceae) is a winter annual herb ranging across much of eastern North America, occurring at the very northern edge of its range in Michigan, where it is listed as a threatened species (MNFI 2020). An *element occurrence* is a distinct observation of an element of biodiversity, such as a rare species. Fort Custer Training Center (FCTC) near Augusta, MI is the stronghold for yellow fumewort in Michigan, with six of twelve confirmed extant element occurrences, and an additional four occurrences shared among the adjacent Fort Custer Recreation Area (FCRA) and Fort Custer National Cemetery (FCNC) (MNFI 2020). All historical occurrences of yellow fumewort were reported from floodplain forests in the Kalamazoo and St. Joseph River watersheds. Despite being a rare native species, all occurrences at FCTC occur in novel habitats dominated by the invasive tree, black locust (*Robinia pseudoacacia*), and have persisted in these habitats since at least 1993 (Legge et al. 1995, Bassett 2016). All occurrences at FCRA and FCNC, and one additional occurrence at the Southwest Michigan Land Conservancy (SWMLC) Chipman Preserve (Chipman) also occur in stands of black locust. Populations of yellow fumewort at FCTC are likely crucial for the persistence of the species in Michigan. However, its fidelity to novel habitats represents a gap in understanding of the species' habitat needs, and ultimately the appropriate approach for management. Much of FCTC, particularly upland habitats, are managed with prescribed fire. Given its typical association with floodplain forests, which historically burned infrequently, it is unclear how yellow fumewort responds to prescribed fire. Here, we report on the results of two related projects, exploring both the connection to its historical floodplain habitat and how it responds to prescribed fire management.

Life history

Yellow fumewort has a winter annual life history. The seeds exhibit morphophysiological dormancy requiring summer temperatures for warm stratification (ca. 35º C day/20º C night) followed by cooler fall temperatures (ca. 20º C day/10º C night) to induce embryo growth and germination (Baskin and Baskin 1994). Individuals germinate in fall, overwinter as rosettes, flower in spring, and die soon after fruit maturation in early summer. In southern Michigan germination begins early September and continues through October, flowering generally begins in late April and continues through May, and senescence occurs by mid- to late-June (Slaughter 2009). Overwintering rosettes face mortality rates of at least 50%, the highest among life history stages (Bassett 2016). Population sizes are spatio-temporally variable. In one study, population density varied from 0 to 64 plants/m^2 (mean 3.8 plants/m^2) from over seven years among three populations (Bassett 2016), and 0 to 23 plants/m^2 (mean 1.4 plants/m^2) over two years among 13 populations (Nuzzo 2005). The long-term viability of seeds is unknown, but seed-banking may be important for the life history of yellow fumewort, especially given temporal variation in population size which may require demographic rescue at population minima. Seeds contain eliasomes, an external starchy attachment attractive to ants, suggesting that ants aid in dispersal, and perhaps in the development of seedbanks. Little is known about yellow fumewort's breeding system as pollinators are rarely observed (Farnsworth 2001).

Habitat

Yellow fumewort occurs in limestone glades, floodplain forests, and occasionally sand savannas from Georgia, north to Connecticut, west to Nebraska, and south to Louisiana (Kartesz 2015). While common in the center of its distribution in the Appalachian states, it is protected or on a watch list in six states and one Canadian province along the periphery of its range- Michigan, Connecticut, New York, Delaware, Nebraska, Georgia, and Ontario (Farnsworth 2001). In

Michigan, yellow fumewort has been reported from at most four southwestern counties: Berrien, Calhoun, Cass, and Kalamazoo (MNFI 2020). Historically limited to floodplain forests in two watersheds in Michigan (Kalamazoo and St. Joseph Rivers), all populations at FCTC occur in a novel, anthropogenic habitat, which is dominated by the non-native tree black locust. FCTC populations occur in areas that were historically either oak-hickory forest or mixed oak savanna and were subsequently farmed, then invaded by black locust after being fallowed (Comer et al. 1995). In addition to black locust, frequent canopy dominants include other pioneer species such as wild black cherry (*Prunus serotina*) and hackberry (*Celtis occidentalis*) (Nuzzo 2005). Ground layer associates mostly include native and non-native annual, winter annual, and biennial herbs, such as cleavers (*Galium aparine*), garlic mustard (*Alliaria petiolata*), and chickweed (*Stellaria media*). Threats include deer herbivory, and to a lesser extent insect herbivory (Nuzzo 2005). Impacts from invasive plants are not clear, although the frequently co-occurring garlic mustard appears to have no effect on yellow fumewort at any life history stage. Garlic mustard competes with other plants by reducing the density of symbiotic mycorrhizal fungi in the soil via root exudates (Cipollini and Cipollini 2016). The absence of garlic mustard impacts on yellow fumewort growth or fitness suggests that yellow fumewort is typical of the family Papaveraceae and in the least not strongly dependent on mycorrhizae.

Association with black locust

It is unclear whether yellow fumewort occurred in the historical oak-hickory forest and mixed oak savanna where black locust now dominates (Comer et al. 1995), dispersed into these sites within the last 100-200 years from adjacent native floodplain habitat, or were introduced intentionally or unintentionally by anthropogenic activities (e.g., movement of military equipment from elsewhere eastern North America). Native to much of the eastern United States from the south of the glaciated regions of Missouri, Illinois, Indiana, Ohio, and Pennsylvania, black locust has been planted widely throughout North America and other temperate regions of the world for land reclamation purposes (Nuzzo et al. 2005, Vitkova et al. 2017).). Black locust invasions impact soil biological activity (e.g., nitrogen cycling) and suppresses or outcompetes a range of taxa from vascular plants to soil microfauna throughout its invasive range (Peloquin and Hiebert 1999, Buzhdygan et al. 2016, Lazzaro et al. 2018). However, yellow fumewort appears to thrive in association with this species. Both black locust and yellow fumewort both possess adaptations that facilitate physiographic or demographic responses to disturbances. Black locust is adapted to low-nutrient conditions by fixing nitrogen, and responds to top-killing (through fire, logging, etc.) by rapid suckering of clones. Yellow fumewort thrives in low-competition environments with high nutrient availability, and as an annual with some seed-banking capacity can respond to sudden pulses in the availability of light, nitrogen and other resources (Nuzzo 2005).

Impact of prescribed fire on yellow fumewort

Prescribed fire is used widely at FCTC to efficiently address many ecological goals, including to reduce invasive species abundances and to increase native species abundance and diversity (FCTC INRMP 2020). The management of vegetation through fire also facilitates the training mission at FCTC. Recruitment in many annual plant species such as yellow fumewort benefits from regular natural disturbances such as fire, but the long-term impacts of fire on yellow fumewort have not been studied. Natural disturbances influence species composition and ecosystem structure in floodplain forests, namely regular flooding and occasional windthrow events (Tepley et al. 2004). These disturbances likely benefit yellow fumewort in its native habitat, but it is not clear whether yellow fumewort responds similarly to a different disturbance, fire instead of flooding, in a novel habitat. The impact of fire on yellow fumewort will likely be direct and indirect, in part mediated by the effect of fire on black locust, as well as soil characteristics, light availability, and the associated ground layer plant community (Figure 1).

Fire consumes leaf litter, creating microsites for seed germination, although fire can also stimulate vegetative growth in perennial herbaceous species (e.g., graminoids) that subsequently outcompete annual species, and alter the availability of soil resources (Walker and Peet 1983, Myers and Harms 2011). Fire can stimulate clonal recruitment and increase stem density in black locust, with unclear indirect impacts on yellow fumewort.

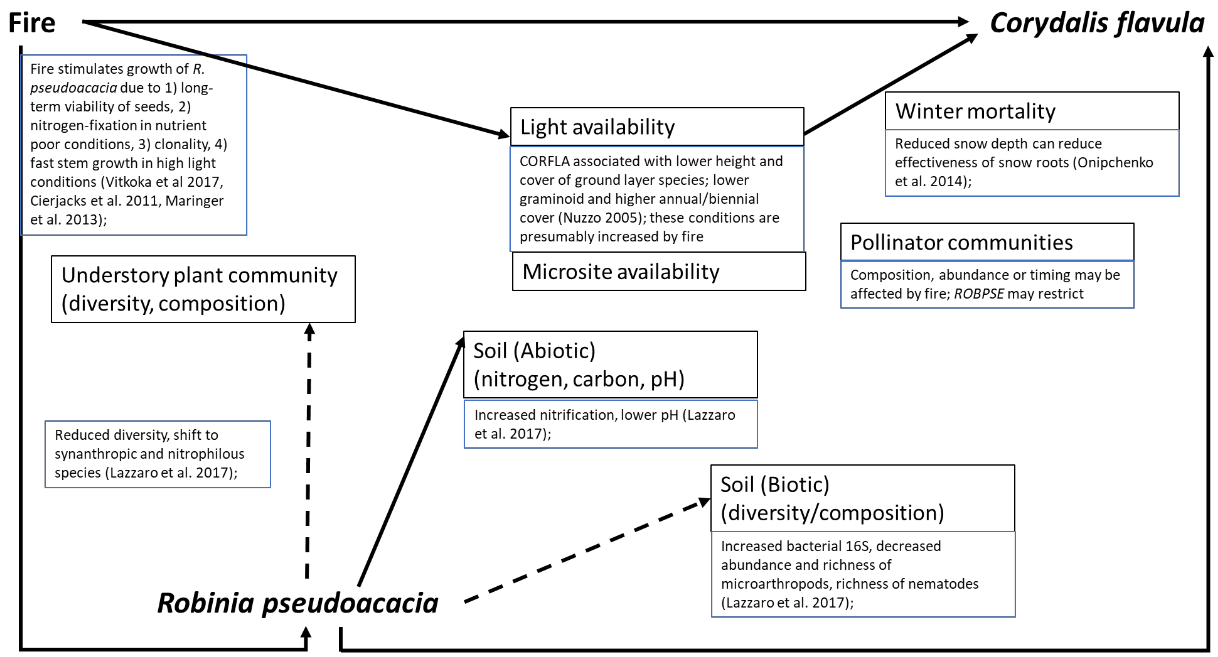

Figure 1. Conceptual model showing hypothesized relationships between fire, yellow fumewort (*Corydalis flavula*), and black locust (*Robinia pseudoacacia*).

Study objectives

I conducted surveys and established monitoring plots to support two lines of inquiry, 1) similarity in habitat conditions between native floodplain populations and black locust populations of yellow fumewort, and 2) impact of prescribed fire on yellow fumewort, both directly and mediated by the effect of fire on black locust. The occurrence of nearby native floodplain populations of yellow fumewort would provide evidence that FCTC populations originated in native floodplain habitat, and therefore constitute a recent adaptation to novel habitat. Furthermore, comparing habitat characteristics in nearby native floodplain populations to those in black locust stands would help to refine metrics for managing yellow fumewort at FCTC. Finally, given the widespread application of prescribed fire at FCTC, it is vital to understand how burning impacts yellow fumewort populations.

The objectives of this study are:

1. Updated the status of several occurrences of yellow fumewort in Michigan.
2. Document new occurrences of yellow fumewort in Michigan.
3. Improve the understanding of links between current occurrences of yellow fumewort in novel habitats at FCTC with the probable historical distribution in adjacent floodplain habitat.

4. Attain an improved understanding of the impacts of fire on yellow fumewort, both directly and indirectly through fire effects on black locust and other habitat components.

Ultimately the goal of this study is to better understand the habitat requirements of yellow fumewort, and as a result, the effectiveness of management efforts. This understanding will increase the long-term viability of yellow fumewort at FCTC and in Michigan. Furthermore, it will increase the effectiveness of the prescribed fire program at FCTC for achieving multiple positive ecological and mission-based outcomes, while reducing negative impacts on species of concern.

Table 1. Summary of yellow fumewort populations at FCTC.

EOID	Training Area	FCTC Pop	Population Estimate	Surveyed
8958	TA1	1	1,000-10,000	06/03/2020
7763	TA9	2a	10-100	05/14/2019
	TA9	2b	1,000-10,000	05/15/2019
	TA7	2c	10,000-100,000	04/10/2019
	TA8-9	6a	10,000-100,000	05/31/2020
2240	TA7	3a	1,000-10,000	04/11/2019
	TA4	3b	100-1,000	04/13/2019
	TA4	3c	10-100	04/10/2019
	TA4	3d	10-100	04/10/2019
6949	TA2	4a	100-1,000	04/16/2019
	TA2	4b	100-1,000	04/16/2019
	TA2	4c	10-100	04/16/2019
	TA2	4d	1,000-10,000	06/05/2020
11994	TA9	5	10,000-100,000	05/14/2019
620	TA9	6b	10,000-100,000	05/10/2019
	TA9	6c	10-100	05/10/2019
	TA9	6d	100-1,000	05/29/2020

Methods

Surveys included population mapping and plot sampling. Population mapping consisted of updating existing and documenting new occurrences of yellow fumewort, and facilitating site selection for plot sampling. In order to investigate the two primary questions in this study, plot sampling focused on describing habitat characteristics in floodplain and non-floodplain populations, and collecting baseline data to track the impacts of fire and habitat differences on yellow fumewort over time.

Population mapping

I conducted a status survey of all known occurrences of yellow fumewort at FCTC and Chipman and conducted surveys in the nearby Kalamazoo River floodplain for new occurrences in spring 2019 (April 10-May 15) and 2020 (May 29-June 5). Spring 2020 surveys were delayed because of travel restrictions due to the COVID-19 pandemic, which were eased in late May. Surveys at FCTC and Chipman were concentrated in areas where yellow fumewort was documented in the MNFI Natural Heritage Database (MNFI 2020), previous published work (Legge et al. 1995, Higman 1997, Nuzzo 2005, Bassett 2016), and through personal communication with land managers at FCTC. The 7,500 acres of FCTC are divided into nine separate training areas (see Figure 2). There are at least 16 separate sub-populations of yellow fumewort grouped into six element occurrences, primarily distributed among four training areas (TA 1, 2, 7, 9), known at FCTC (Bassett 2016, MNFI 2020). Floodplain surveys were concentrated in accessible areas of the Kalamazoo River floodplain, including FCRA, FCNC, and the SWMLC Augusta FloodplainEmmons Preserve (Figure 2). Surveys were planned for Kalamazoo County's River Oaks Park, but the park was inaccessible in spring 2020 due to COVID-19. I conducted meander surveys in potential or known habitat and mapped every yellow fumewort population using Avenza (version 3.12) on a Samsung Galaxy 8 tablet. For each population at FCTC, I estimated population size within the following ranges: 1-10 individuals; 10-100; 100-1,000; 1,000-10,000; 10,000-100,000 (Table 1).

Plot sampling

In fall 2020, I established nine plots distributed among FCTC (4 plots), FCRA (3 plots), and Chipman (2 plots). Plot establishment was initially planned for spring 2020 but was delayed due to travel restrictions related to the COVID-19 pandemic. Three kinds of plots were established: plots with prescribed fire planned for 2021 (burn plots; 2 at FCTC, 1 at Chipman), plots adjacent to the Kalamazoo River floodplain (floodplain plots, 3 at FCRA), and control plots (2 at FCTC, 1 at Chipman) (Figure 3, Table 2). I obtained burn plans through personal communication with land managers at FCTC (Ryan Koziatek, Kalamazoo Nature Center; Michele Richards, FCTC) and Chipman (Mitch Lettow, SWMLC). Burn plots were established to test hypotheses about the effects of prescribed fire on yellow fumewort, black locust, and their interaction. Floodplain plots were established to compare habitat and yellow fumewort demography, between populations in the assumed historical habitat of yellow fumewort in the Kalamazoo River floodplain, and populations in the core of its current habitat in current black locust stands. Control plots were established in current black locust stands for which no burns were planned for 2021, to serve as reference sites for both floodplain and burn plots.

I selected sites that surveys indicated would support sufficiently large populations of yellow fumewort to confidently estimate demographic parameters. In September 2020, I established a 20 m X 50 m (1,000 m^2 or 0.1 ha) rectangular plot in each site. Using the center of each

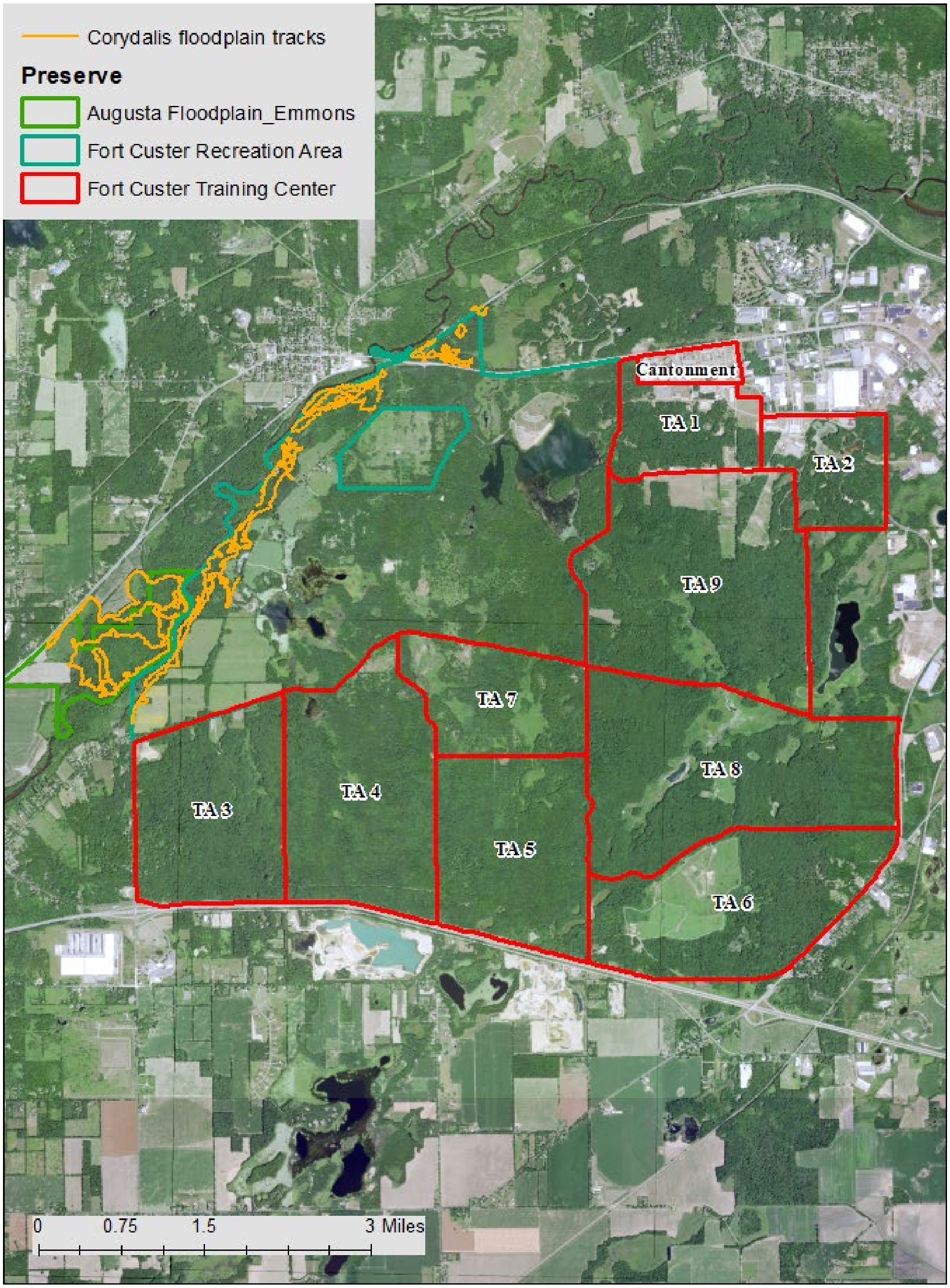

Figure 2. GPS tracks showing areas within and adjacent to Kalamazoo River floodplain surveyed in Fort Custer Recreation Area and Augusta Floodplain-Emmons Preserve.

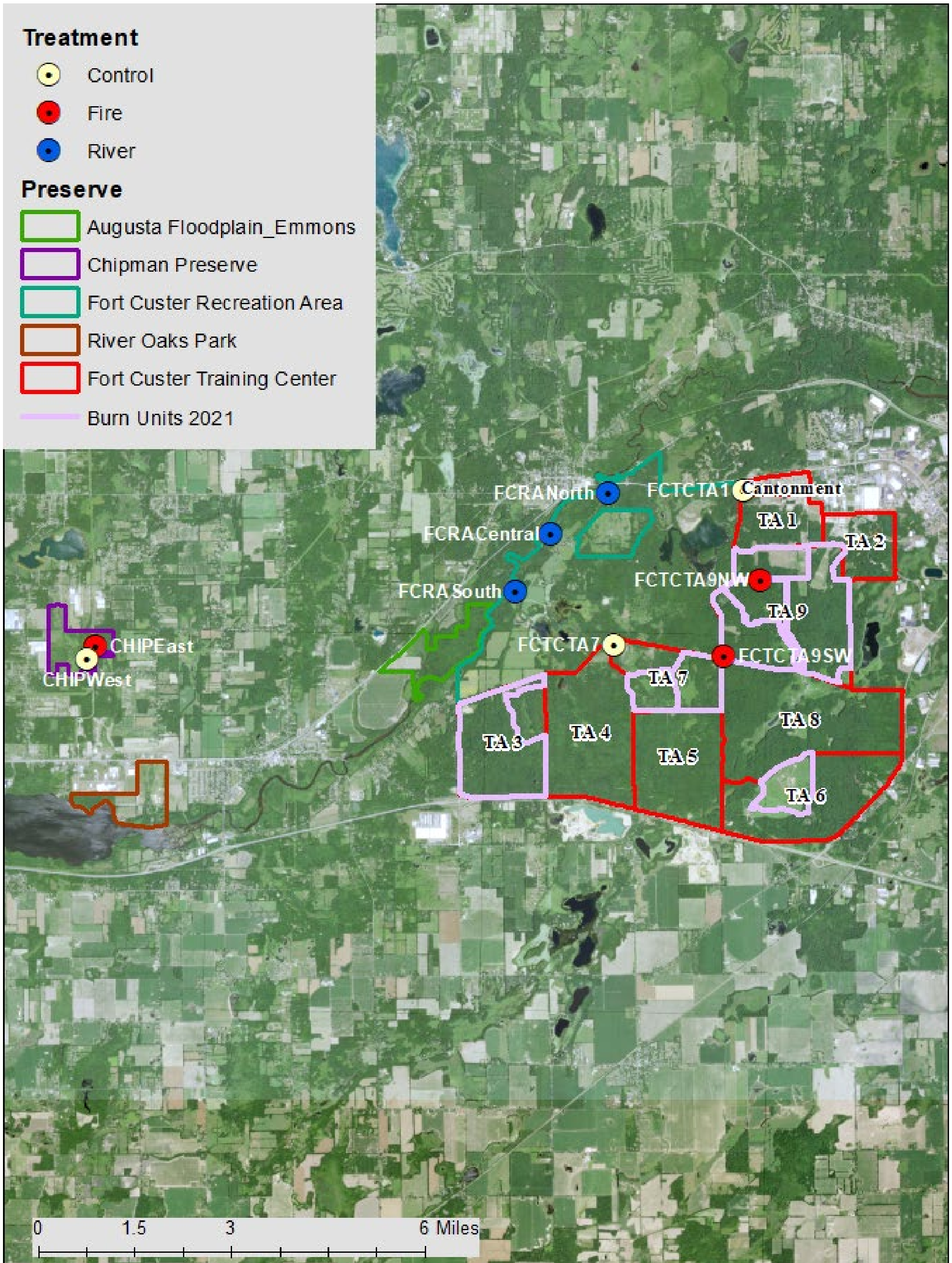

Figure 3. All accessible areas with potential to support yellow fumewort populations. Location of plots sampled ('Treatment' in legend) also shown, and burn units at FCTC with prescribed fires planned for spring 2021.

counter-clockwise direction. As a result, the origin is located in the bottom right of each plot.

I collected data on plant community and structural attributes of each plot. Structural attributes included canopy and midstory density, while community attributes include canopy, midstory, and ground layer plant species composition (including yellow fumewort), leaf litter, and soils. I recorded the diameter-at-breast-height (DBH) and identity of all trees (woody stems > 10 cm DBH) in the whole plot. I counted the number of stems for each species of midstory shrubs and saplings (woody plants under 10 cm DBH and at least 1.0 m tall) in four, 2-meter-wide belt transects, centered on the 10-,20-,30-, and 40-m mark along the long (50m) axis of each plot. I sampled ground layer, leaf litter, and soils in 20, 50X50 cm quadrats. One half of these quadrats were established to estimate ground layer habitat characteristics for each plot ("habitat quadrats", n=10), and one half were established to monitor yellow fumewort ("Corydalis quadrats", n=10). I established habitat quadrats at the origin, then moving clockwise, 10m, 30m, 50m (upper right corner), 60m, 70m (upper left corner), 80m, 100m, 120m (bottom left corner), and 130m. I used a stratified sampling design to locate Corydalis quadrats, to reduce bias while ensuring each quadrat contained at least five individuals. After splitting each plot into ten, 10 X 10 m subplots, I placed a quadrat in each subplot parallel to the axes of the plot, in a location maximizing the number of yellow fumewort seedlings. If a subplot contained an insufficient density of yellow fumewort, I placed the associated quadrat in an adjacent subplot. Within each habitat and Corydalis quadrat, I recorded the following: 1) the identity of each vascular plant species; 2) the percent cover of leaf litter, vegetation, bare soil, rocks, woody debris, moss/lichen/fungi, and tree trunk (summing to 100); 3) leaf litter depth on all four inside corners of each sub-plot to the nearest 0.5 cm; and 4) one 20-cm-deep soil core on the outside midpoint of each side the subplot. Additionally, I recorded the number of yellow fumewort seedlings in each Corydalis quadrat.

Table 2. Summary of yellow fumewort sampling plots. Dominant trees: ACESAU = *Acer saccharum*, CARCOR = *Carya cordiformis*, CELOCC = *Celtis occidentalis*, PRUSER = *Prunus serotina*, ROBPSE = *Robinia pseudoacacia*. RIV = Relative importance value, (relative basal area + relative abundance)/2. *See Figure 3 for plot locations.*

Plot	treatment	Location	Lat	Long	Dominant trees (RIV)	Soil texture
CHIPEast	Fire	Chipman Preserve	42.3076	-85.4575	ROBPSE (30.84), PRUSER (27.65)	loamy sand
CHIPWest	Control	Chipman Preserve	42.3056	-85.4595	PRUSER (57.56)	sandy loam
FCRACentral	River	Fort Custer Recreation Area	42.3264	-85.3552	PRUSER (24.26)	loamy sand
FCRANorth	River	Fort Custer Recreation Area	42.3332	-85.3425	ROBPSE (61.06)	sandy loam
FCRASouth	River	Fort Custer Recreation Area	42.3168	-85.3632	CELOCC (21.02), CARCOR (18.9)	loamy sand
FCTC1	Control	Fort Custer Training Center	42.3335	-85.312	ROBPSE (41.23)	loamy sand
FCTC7	Control	Fort Custer Training Center	42.308	-85.3411	ACESAU (42.73)	sandy loam
FCTC9NW	Fire	Fort Custer Training Center	42.3185	-85.3082	ROBPSE (32.21), PRUSER (26.92)	loamy sand
FCTC9SW	Fire	Fort Custer Training Center	42.306	-85.3165	PRUSER (63.33)	sandy loam

Data analysis
I conducted two sets of analyses. First, I assessed variation in habitat characteristics across all plots, including the correlation with yellow fumewort populations. These analyses are useful for drawing conclusions about the ecology of yellow fumewort habitat overall. Second, I compared community and structural attributes among the three different types of plots, River, Fire, and Control. These analyses are useful for establishing how baseline variation is distributed among plot types, so that changes to yellow fumewort populations through time can be placed in context. The analyses presented in this report are largely descriptive and exploratory, having been conducted on baseline data that will be used to track and understand yellow fumewort changes through time, in response to fire and in response to habitat differences.

I used principle components analysis to better understand relationships between ground layer variables (% cover of vegetation, leaf litter, bare ground, woody debris, rocks, moss and fungi, and trees, and litter depth), for habitat quadrats and Corydalis quadrats, separately. Principle components analysis reduces a large number of variables into a smaller set of composite variables, or principle components axes, that express the covariation among that set of variables. The amount of variation for each variable relative to each other variable that is represented by an axis is referred to referred to as that variable's "loading" on that axis. I used loadings on principle components axes to explore how sites were differentiated according to ground layer attributes. The first, second and third principle component axes for habitat quadrats account for 24%, 19%, and 15% of the variance, respectively, for a cumulative total of 57% of the variance. The first axis (habitat PC1) is a positive to negative gradient of moss cover to leaf cover and depth. The second axis (habitat PC2) is a gradient from woody cover to vegetative cover. The third axis (habitat PC3) is a gradient from bare ground and tree trunk cover to woody debris, moss, and rock cover. The first, second and third principle component axes for Corydalis quadrats account for 30%, 17%, and 14% of the variance, respectively, for a cumulative total of 61% of the variance. The first axis (Corydalis PC1) is a positive to negative gradient of leaf cover and depth to moss cover. The second axis (Corydalis PC2) is a gradient from woody cover to vegetative cover. The third axis (Corydalis PC3) is a gradient from woody debris cover to bare ground and rock cover.

Table 3. Pearson's correlation coefficients between number of individuals of *Corydalis flavula* and ground cover variables in *Corydalis* plots.

	Corydalis	veg.pct	leaf.pct	bare.pct	woody.pct	moss.pct
veg.pct	-0.10					
leaf.pct	0.14	**-0.50**				
bare.pct	0.05	-0.09	**-0.31**			
woody.pct	-0.09	**-0.23**	**-0.20**	0.05		
moss.pct	-0.12	-0.02	**-0.69**	-0.02	-0.01	
leaf.depth	-0.10	-0.04	**0.57**	**-0.45**	-0.08	**-0.46**

I compared the fit of a set of linear regressions to test how the density of yellow fumewort was correlated with ground layer attributes. I fit a generalized linear mixed-effects model with Corydalis PC1, Corydalis PC2, and Corydalis PC3 as fixed effects, and site as a random effect due to non-independence of plots. It can be hard to interpret effects of principle component axes, so I constructed a similar model including leaf depth, and percent cover of vegetation, bare ground, woody debris, and moss. Percent cover of rocks and tree trunks were excluded to simplify the model, as there were only three plots containing values for these variables. Percent cover of leaf litter was excluded to reduce multicollinearity, as this variable is highly correlated with many other variables and likely to lead to spurious results (Table 3). Variance inflation factors were mostly > 6 in a model including percent cover of leaf litter, and all < 2 in the model excluding this variable. I used AICc to compare model fit for these two models, as well as additional single fixed-effects models for all variables in these two models, including a null model including no fixed effects.

Table 4. Summary data for each treatment type (River, Fire, Control), and differences between treatment groups tested by ANOVA.

	Group means						ANOVA		Range	
	River	SE	Fire	SE	Control	SE	$F_{2,6}$	p	min	max
COMMUNITY										
# locust trees	22.33	15.86	10.33	4.70	7.00	7.00	0.60	0.58	0	54
Total locust DBH	173.33	132.50	122.67	61.57	75.67	75.67	0.26	0.78	0	438
Corydalis quadrats										
Corydalis flavula	192.67	17.40	102.67	30.21	133.00	27.47	3.1937	0.11	54	221
Mean SR/m2	8.21	0.76	7.52	0.26	7.91	1.39	0.142	0.87	6.09	10.64
Transect SR	31.33	1.45	28.00	2.52	27.33	1.86	1.1589	0.38	25	34
Simpon's diversity	10.79	0.60	10.32	0.56	10.98	0.95	0.2211	0.81	9.20	12.69
Habitat quadrats										
Mean SR/m2	6.07	0.09	5.03	0.23	5.53	1.30	0.46	0.65	3.3	7.8
Transect SR	23.33	2.73	21.67	1.86	18.33	3.18	0.93	0.45	13	27
Simpon's diversity	8.68	0.43	7.72	0.41	8.56	1.23	0.45	0.66	6.15	10.18
STRUCTURE										
# shrub stems	151.33	21.14	181.67	83.67	68.67	7.88	1.37	0.32	53	349
# tree stems	80.33	6.36	53.67	10.09	53.67	11.02	2.70	0.15	32	93
total basal area (ft^2/A)	119.50	9.25	159.10	26.55	127.35	18.76	1.16	0.38	98.16	194.56
%sand	75.94	2.16	74.68	3.72	76.25	2.69	0.08	0.92	68.1	81.4
%silt	21.73	2.14	23.06	3.79	14.18	1.46	3.26	0.11	11.36	29.79
%clay	2.33	0.03	2.26	0.07	9.58	3.63	4.01	0.08	2.13	13.64
pH	5.57	0.55	5.20	0.12	5.20	0.45	0.26	0.79	4.5	6.3
organic matter (%)	2.57	0.20	2.53	0.15	2.43	0.17	0.16	0.86	2.1	2.9
Corydalis quadrats										
Leaf depth (cm)	1.22	0.28	1.13	0.30	0.71	0.08	1.2536	0.35	0.59	1.63
% bare ground	2.50	1.80	3.33	1.48	6.83	3.11	1.0477	0.40	0	13
% vegetation	16.67	1.88	27.00	2.93	19.17	2.32	4.9905	0.05	13.5	31.5
% leaf cover	70.50	5.39	54.83	7.49	50.83	9.799376	1.7893	0.25	32.5	80.5
Habitat quadrats										
Leaf depth (cm)	1.08	0.37	1.08	0.23	1.22	0.53	0.04	0.96	0.58	2.26
% bare ground	6.33	2.62	6.50	0.50	9.50	2.84	0.63	0.57	3.0	13.5
% vegetation	17.17	1.83	29.17	3.48	22.00	5.25	2.54	0.16	13.5	35.5
% leaf cover	50.83	9.69	48.67	5.49	46.00	6.37	0.11	0.90	35.5	69.5

I tested for differences in select community and structural attributes among treatments (River, Fire, Control) using ANOVA (Table 4). I tested for differences in canopy and mid-story attributes, including the total number of shrub stems, total number of tree stems, total basal area (ft^2/A) (structural attributes); and number of individuals of black locust trees and the total DBH of black locust (community attributes). I tested for differences in ground layer attributes separately for habitat and Corydalis quadrats, including leaf depth and percent cover of leaf litter, bare ground, and vegetation cover (structural); and mean quadrat species richness, richness across all quadrats, and Simpson's diversity (1/D, where D=$\sum_i^S p_i^2$, where p_i is the frequency of each 1 to S species at a site) (community). Among Corydalis quadrats, I also tested for differences in yellow fumewort density.

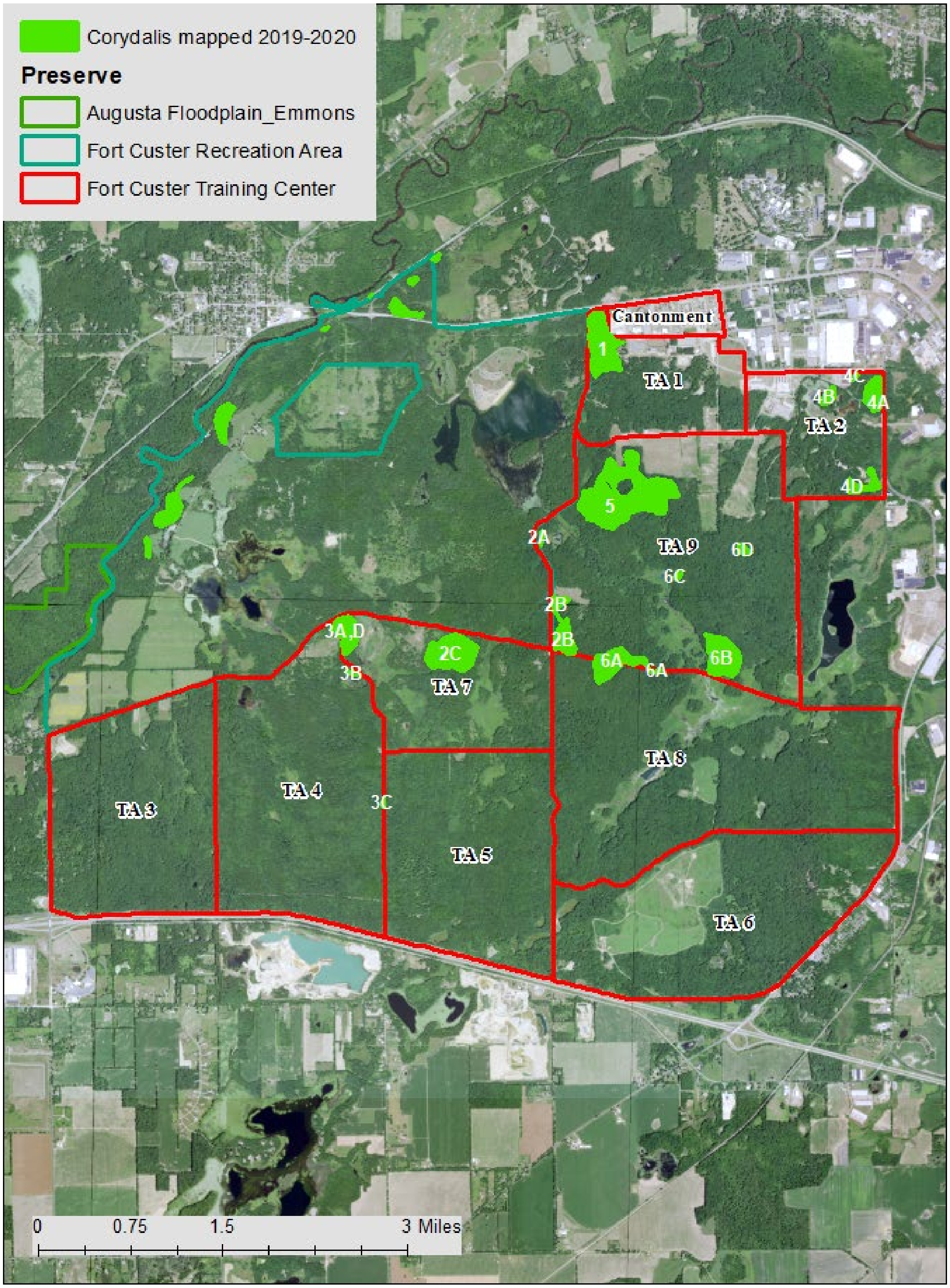

Figure 4. Yellow fumewort populations mapped during this study. See Table 1 for alpha-numeric designations of populations at FCTC.

Results

Population Mapping
All known sub-populations of yellow fumewort at FCTC were relocated and mapped (Figure 4). One additional sub-population was located and mapped in Training Area 9 (sub-population 6D; Table 1, Figure 4). Each sub-population varied in size from less than 100 individuals to several 10,000s of individuals (Table 1). Population estimates were consistent with those made in recent years (Bassett 2016). One new element occurrence was documented near the Kalamazoo River in FCRA, comprised of three relatively distinct sub-populations (Figure 4). Individuals of yellow fumewort here were restricted to stands of black locust and did not occur within the floodplain itself. Despite surveys covering over 100 acres of relatively high-quality floodplain, including mucky bottoms, sandy and silty ridges, levees, and banks, I observed no true floodplain populations of yellow fumewort.

Plot sampling
Model selection results indicate that models including the third principle components axis of ground layer attributes from Corydalis quadrats best fit the data, while the first and second axes were not associated with yellow fumewort density (Table 5). The third axis was negatively correlated with yellow fumewort density ($p<0.01$) but explained only 10% of the variation in density. This suggests that yellow fumewort density is positively correlated with the percent cover of bare ground and rocks, and negatively correlated with the percent cover of woody debris (Figure 5). Random variation between sites explained more variation in yellow fumewort density than fixed effects (marginal pseudo-R^2 = 0.10, variation explained by fixed effects; marginal pseudo-R^2 = 0.26, variation explained by both fixed and random effects). Among individual ground layer attribute models, only the leaf depth model fit the data better than the null model, although leaf depth was not correlated with yellow fumewort density ($p=0.51$, marginal pseudo-R^2 = 0.01).

Table 5. Model selection results. Models with ΔAICc < 2.0 fit the data equally well. Marginal pseudo-R^2 = variation explained by only fixed effects, conditional pseudo-R^2 = variation explained by both fixed and random effects. *Df*= degrees of freedom; *weight* = Aikake weight (larger values correspond to better-fitting models).

				pseudo-R^2	
Model	**ΔAICc**	**df**	**weight**	**marginal**	**conditional**
PC3	0	4	0.562	0.10	0.26
PC1 + PC2 + PC3	0.7	6	0.399	0.11	0.27
leaf depth	7	4	0.017	0.01	0.21
null	8.8	3	0.007	0	0.20
PC1	9	4	0.006	0.01	0.22
PC2	9.3	4	0.005	<0.001	0.20
woody debris	12	4	0.001	0.01	0.21
moss + fungi	12.2	4	0.001	0.02	0.23
bare ground	12.6	4	0.001	<0.001	0.21
vegetative cover	13.8	4	<0.001	<0.001	0.20
all ground layer	20.4	8	<0.001	0.06	0.24

Community and structural attributes varied between treatment types (River, Fire, Control), but none of these differences was statistically significant (ANOVA, all $p>0.05$) (Table 4). A few attributes showed a tendency to be higher in one treatment type (according to a less conservative $p<0.15$, due to small sample size), although post-hoc contrasts confirmed that these differences were not statistically significant (Tukey's HSD, adjusted $p>0.10$). Among these, percent silt tended to be lower ($p=0.11$) and percent clay tended to be higher ($p=0.08$) in Control plots; yellow fumewort density (0.11) and total number of tree stems (0.15) tended to be higher in River plots; and percent vegetative cover in habitat quadrats ($p=0.05$) tended to be higher in Fire plots. Ultimately, these data provide a baseline to measure changes in response to management and succession among these groups. Summaries showing means of select community and structural attributes are summarized in Table 4.

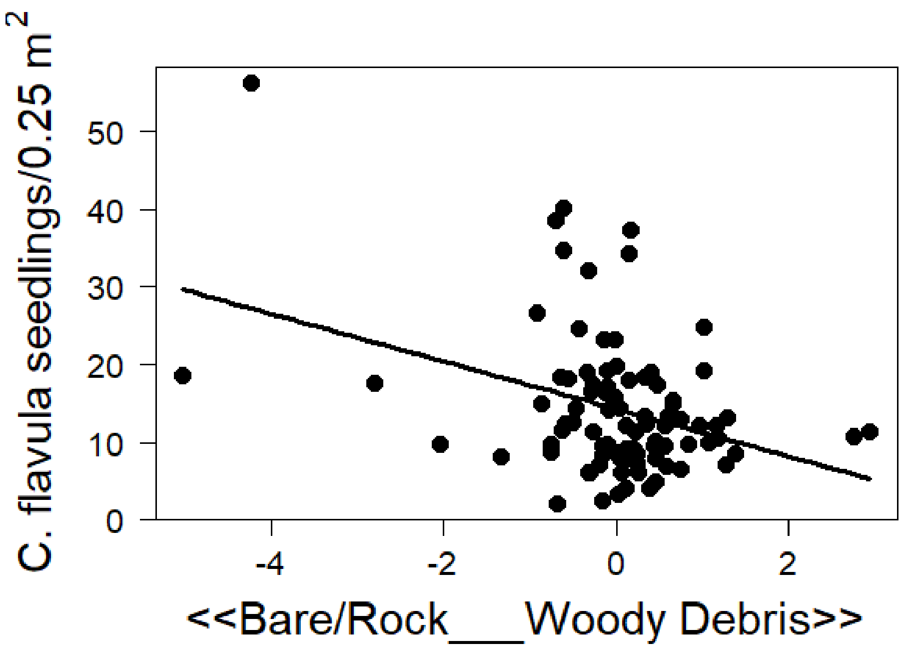

Figure 5. Yellow fumewort seedlings decrease along ground cover gradient from bare ground and rocks to woody debris. Ground cover gradient modeled as principle component axis (*see PC3 in text)*.

Discussion

This study had four objectives with the overarching goal of improving management outcomes for the state threatened herb, yellow fumewort. The objectives were to update existing occurrences in anthropogenic black locust stands at FCTC, document new occurrences in or near the Kalamazoo River floodplain, explore ecological linkages between anthropogenic and floodplain populations, and to study how the application of prescribed fire affects yellow fumewort populations. Over 2019-2020, I completed the first three objectives, and collected baseline data that is necessary to achieve the fourth objective.

Yellow fumewort populations at FCTC, FCRA, and FCNC appear to be stable, with a high likelihood of persisting for the next 20-30 years. The association of this state threatened species with high densities of the invasive tree black locust and invasive herb garlic mustard does not appear to reduce the fitness of these populations, and may be beneficial. Populations within FCTC have been surveyed annually, and despite minor fluctuations have maintained consistent numbers or increased (Bassett 2016, *personal observation*). Furthermore, I documented new populations during this study, including an occurrence near but not within the Kalamazoo River floodplain. All extant occurrences, including those newly documented during this study, are associated with black locust. Occasional patches or individuals of yellow fumewort occurred in patches of sugar maple, wild black cherry. Without exception, these patches or individuals occurred on the fringes of large stands of black locust supporting large yellow fumewort populations, or in small gaps in the canopy of black locust dominated by other species.

Relationship between Kalamazoo River floodplain and extant yellow fumewort occurrences

I observed no populations of yellow fumewort in the portion of the Kalamazoo River floodplain directly adjacent to FCTC, FCRA, and FCNC. This result provides necessary, but not sufficient evidence to disprove the hypothesis that FCTC populations of yellow fumewort originated via dispersal from the Kalamazoo River floodplain. Yellow fumewort was documented downstream of FCRA along the southern floodplain in a “rather open woodland” in a “wooded river bank” as recently as 1930s (Hanes and Hanes 1947). This stretch of floodplain has been submerged under Morrow Lake, a dam pond, since 1941 (Wesley 2005). Regardless, yellow fumewort occurred very nearby in the Kalamazoo River floodplain, at least historically, and may still persist.

At the outset of this study, a primary goal was to compare the ecology of forest stands in sandy uplands dominated by black locust, to forest stands in floodplains on presumably siltier soils with different canopy dominants. The absence of extant floodplain populations leaves many questions unanswered, such as whether adaptations to floodplain habitats benefit yellow fumewort in black locust stands. Delayed seed germination (seed-banking) in another winter-annual species of floodplain forests, blue-eyed Mary (*Collinsia verna*), has major demographic effects and appears to be vital for population persistence (Kalisz 1991, Kalisz and McPeek 1992). In particular, seeds of different ages germinate at different times and have different growth rates. This seedbank age structure maintains population growth in response to a variable disturbance regime, namely the timing of spring flooding. It is possible that yellow fumewort has similar adaptations. In the absence of fire, however, soil and litter disturbance in black locust stands does not naturally occur at the scale of flooding and deposition in floodplain forests. However, black locust suppresses or modifies soil biological activity, and the prevalence of yellow fumewort in black locust stands may be at least in part attributed to adaptations to changing soil microbial and microfaunal communities (Peloquin and Hiebert 1999, Buzhdygan et al. 2016, Lazzaro et al. 2018).

Relationship between yellow fumewort and fire

Adaptation to frequent disturbance may translate to increased fitness of yellow fumewort populations with regular prescribed fire. Modelling the correlation of ground layer attributes with yellow fumewort density suggested that bare ground (and to a lesser degree, rocks) is associated with higher densities and woody debris is associated with lower densities. The association of yellow fumewort with bare ground suggests that fire may facilitate recruitment by burning off leaf litter (and possibly woody debris) and increasing microsites for germination. However, this interpretation/conclusion should not be overstated. The third principle component axis (Corydalis PC3) explained only 14% of the variation in ground layer attributes, and modelling effects of Corydalis PC3 explained only 9% of the variation in yellow fumewort density. Understanding the relationship between yellow fumewort and fire, as mediated through ground layer attributes and black locust, requires both the experimental application of prescribed fire and collecting data on all life history stages of yellow fumewort.

Future Steps

Further sampling efforts will be necessary to draw substantive conclusions that will improve the management outcomes in habitats containing yellow fumewort. First, repeated sampling of plots established in Fall 2020 is necessary to understand demographic differences of yellow fumewort in River, Fire, and Control plots. Sampling of winter survivorship and fecundity (e.g., number of seeds, fruits or flowers) in Spring 2021 will provide a much more complete picture of differences between plot types, particular with and without prescribed fire. Second, additional surveys along the Kalamazoo River may uncover populations of yellow fumewort in areas that have not been surveyed to date.

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Appendix 1. Canopy composition and basal area summary

site	CHIP East	CHIP West	FCRACentral	FCRANorth	FCRASouth	FCTC1	FCTC7	FCTC9NW	FCTC9SW
treatment	**Fire**	**Control**	**River**	**River**	**River**	**Control**	**Control**	**Fire**	**Fire**
Acer negundo	16.14								6.14
Acer rubrum			1.82						
Acer saccharum		10.11		7.69	1.66		**42.73**		
Carya cordifomis			1.06		**18.90**				
Celtis occidentalis					**21.02**	19.80	3.52		2.53
Cercis canadensis					0.98				
Crataegus sp.			0.84			0.97			
Fraxinus americana									2.40
Gleditsia triacanthos			15.44		1.04				
Juglans nigra			0.89		12.45		23.39	2.33	
Morus alba		2.11	0.94		4.19				
Pinus sylvestris	2.05								
Prunus avium		1.44							
Prunus serotina	**27.65**	**57.56**	**24.26**	19.42	10.77	16.13	30.36	**26.92**	**63.33**
Pyrus communis						1.01			
Quercus bicolor			2.08	0.84					
Quercus rubra					0.98				
Quercus velutina	15.82		5.87	2.85		1.01			1.20
Rhamnus cathartica			3.56						
Robinia pseudoacacia	**30.84**		5.24	**61.06**	8.97	**41.23**		**32.21**	2.01
Robinia pseudoacacia snag		15.95	15.01	6.31	11.07	16.18		6.20	
Sassafrass albidum									4.73
Snag	7.49	7.35	15.22		2.86	3.66		9.49	11.78
Tilia americana					0.88				
Ulmus americana		4.62	7.79	1.84	4.23			22.85	5.88
Unknown		0.88							