

## Human-mediated impacts on *Iris versicolor* L. populations across northern Michigan

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### ABSTRACT

Anthropogenic effects on the natural world have been at the forefront of the scientific conscience for at least the past 50 years. A measurable proxy for human impact on environment is the health and distribution of populations of organisms, especially plant species. In Michigan, a good model plant species for assessing human environmental impact is *Iris versicolor* L., a distinctive wetland plant native to eastern North America. We mapped location data for 89 *I. versicolor* populations and visited a subset of 30 populations to assess population presence/absence, total area of current populations, co-occurring plant species with an emphasis on invasive and aggressive species, pH, electrical conductivity, and texture of soils; and proximity of sites to human disturbances like roads and buildings. Aggressive species appear to have the most significant impact on *I. versicolor* presence/absence, especially *Typha* species both native and introduced to Michigan. *I. versicolor* appears to be most vulnerable to factors leading to its disappearance at the southern margin of its range, perhaps due to a synergistic effect between human disturbances, invasion of aggressive species, and warming climate; more research should be conducted to substantiate these findings. Continued visitation of these sites would serve to inform relationships between *I. versicolor*, other native and invasive species, humans, and our environment.

Keywords: *Iris versicolor*, Michigan, human impacts, ecology, conservation, herbaria, presence/absence

## **Introduction**

Anthropogenic effects on the natural world have been at the forefront of the scientific conscience for at least the past 50 years (Carson, 1962). In that time, research has been conducted on the impacts of human activity on abiotic and biotic factors of the environment, including climate and weather, biogeochemical cycling, and abundance of biodiversity. The overall findings have been considered rather bleak – it is known that human activities have caused vast changes to the atmo-, litho-, hydro-, and biospheres since at least the Industrial Revolution, such that we have ushered in a new geological epoch, moving from the Holocene to the “Anthropocene” (Crutzen, 2006; Steffen et al., 2007; Steffen et al., 2011; Lewis & Maslin 2015).

For experts in the natural sciences, the Anthropocene is marked as the “sixth mass extinction event”, as huge swaths of biodiversity are becoming endangered or extinct due to direct or indirect human activities. These activities include habitat destruction in the wake of constructing roads, agricultural land, and settlement areas; introductions of alien and invasive species via human migrations and transportation; and changes to annual global temperatures and precipitation patterns due to climate change (Pryor *et al.*, 2014; Seto *et al.*, 2011; Jacquemyn *et al.*, 2010; McGinley, 2010; Brooker, 2006). Species that have not drastically decreased in numbers may instead be extirpated from current habitats, shifting their ranges northward or to higher elevations to escape the impacts of these activities – particularly rising temperatures or other climatic effects (Thomas et al., 2001; Lesica & McCune, 2004; McKenney et al., 2007; Kelly & Goulden, 2008; Fosså et al., 2010).

Because of these very real dangers to global biodiversity, taxa that are endangered or at risk are the focus of conservation research, leading to large amounts of literature concerning human impacts on sensitive species (Channell & Lomolino, 2000; Male & Bean, 2005; DeCasare et al., 2010). However, common species are seldom examined for the effects of human activities on their population sizes and abundance. Species of “least concern” may be able to recolonize quickly in the wake of human disturbances, compete effectively against aggressive species, or tolerate changes in land use or climatic variables, but it is difficult to predict which strategies might be employed by different species. Furthermore, due to their “least concern” status, populations of these common species may be disappearing with researchers remaining unaware.

Studying populations of organisms over time can present challenges, especially for mobile species that require ample time, resources, and luck to encounter individuals and adequately estimate population size. Sessile populations such as plants can mitigate these complications. Furthermore, for long-term studies of plant population abundance throughout a given region, a wealth of initial data is already present in the form of herbaria. These institutions document the habitats and distributions of plants from across the globe, representing a rich history of botanical biodiversity spanning several centuries. Herbaria are increasingly valuable databases as our landscapes undergo pronounced changes – yet, how often are populations represented in herbarium specimens revisited and reexamined? By revisiting the locations from which herbarium specimens were collected, it is possible to examine the ways in which these populations have reacted to environmental change through time, or even if they are still present today.

To effectively examine plant population response to human activities that impact the environment of Michigan, a good candidate species would possess: 1) a perennial and riparian habit, such that populations would persist year to year regardless of changes in annual precipitation, while also maintaining sensitivity to water and soil quality which may be affected by nearby roads and farmland; 2) a described habitat range tending toward northern latitudes, so that a response to rising temperatures may be observed; and 3) an abundance of specimens with varying collection dates throughout the research area, here the state of Michigan. The species *Iris versicolor* L. fulfills each of these criteria.

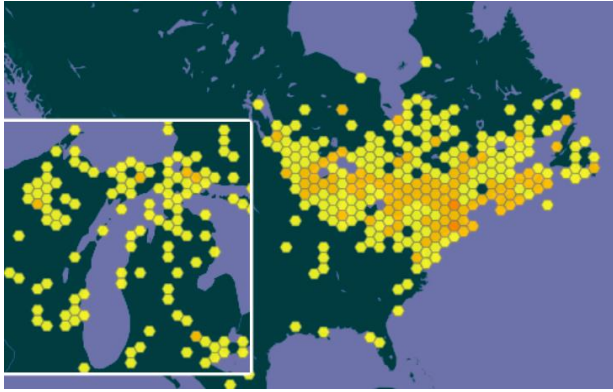


Figure 1. Native range of *Iris versicolor* in the northeast of North America, from collection data spanning 1822 to present. Inset of Michigan collection data. Retrieved from GBIF (2019).

*Iris versicolor*, also known as the northern or harlequin blue flag iris, is a common monocot species of the family Iridaceae (Wilson, 2009). Native to northeastern North America with introductions in Europe and New Zealand, it is a northern species that prefers colder climates (Figure 1). It can often be found in wetland habitats with other riparian taxa. It can be easily identified by its long basal leaves and showy purple 3-merous perianth, or 3-chambered capsule with large, uniformly papillate seeds (Anderson, 1936; Figure 2). It tends to grow in large mats along rivers, lakes, or ditches, reproducing via clonal individuals using its thick spreading rhizomes, but it can also be pollinated by a variety of insects and disperse its seeds along waterways (Lovell, 1899; Needham,

1900).

Because of these characteristics of *I. versicolor*, we predicted that we could reliably relocate the sites of historic *I. versicolor* populations using herbarium specimen data. Furthermore, we predicted that some populations – particularly those at more southern latitudes, closer to human disturbances, or with higher incidence of invasive species in the habitat – would be absent, and would not be found. We also predicted that populations found at their historic sites would inhabit soils with consistent conditions of soil texture, pH, and electrical conductivity, especially when compared to sites where *I. versicolor* populations were absent.



Figure 2. Images of *Iris versicolor* taken in the field. Left: Pressing of *I. versicolor* collected 2017, showing long basal leaves, purple-red flushed base, and perianth. Center: perianth of *I. versicolor*. The larger “falls” are modified sepals with yellow nectar guides. Top right: immature capsules showing three chambers. Bottom right: Mature dehiscent capsule with seeds exposed (image credit: Mason, 2005).

## Methods

### Site establishment

In October 2016 we compiled locality data from specimens from the University of Michigan Herbarium (MICH) for *Iris versicolor* populations in the state of Michigan. Locations that could be determined from herbarium labels were plotted approximately using an ArcGIS map. In total, seventy-four (74) sites were mapped.

We defined the University of Michigan Biological Station as the primary research base for this study and removed 32 of the 74 sites from the visitation itinerary due to considerable distance from the base. Nine additional sites were excluded later based on incomplete location data (see “Certainty of site location”) or inability to access the site. Of the remaining sites, 26 were successfully visited by the first author between June and August of 2017. Collections, population presence or absence at each site, and removed sites were also plotted on the ArcGIS map.

Subsequently, 15 additional sites were located using specimens listed in iDigBio (<https://www.idigbio.org/portal/search>), and five of these were successfully visited in the summer of 2018. Seven sites originally visited in summer 2017 were also re-visited and examined for changes. Thus, we sampled a total of 30 sites, seven of them in both field seasons. A table of the herbarium data initially compiled as well as the subset sampled can be found in the Appendix.

Site visitation and location were facilitated using locality approximations, ArcGIS, and Google Maps leading up to and at each site. Location data derived from herbarium labels were variable in quality, and sometimes led to difficulty in recognizing a particular location or population in the field as a “site”; for example, voucher data describing the “north shore of Rennie Lake” naturally had less site specificity than “500 feet east of State Street” or latitude/longitude coordinate data. Thus, time devoted to locating *I. versicolor* at a site was generally one hour, with the population declared absent only when sufficient confidence in the correct locality of a site had been achieved (see “Certainty of site location”). A DNR research permit (PRD-SU-2017-042) was obtained for work on state lands. For sites located on private property, access was requested via spoken landowner approval.

### Site visitation procedures

Once a population of *I. versicolor* was located, we recorded the site number, date, and time of visitation, then measured the dimensions of the population ( $m^2$ ). The size of exceptionally large populations expected to exceed an area of 200  $m^2$  (such as populations surrounding a lake or along a long stretch of road) was extrapolated along the proposed perimeter (lake) or length (road) on a case-by-case basis. The clonal nature of *I. versicolor* led to clumps of leaf rosettes and blooming stems in close proximity; however, distances between clumps were often variable. The first author counted the number of clumps in each population, measured the dimensions of each clump, and calculated the average clump area for each population. A second measure of population size was made by counting vegetative leaf rosettes and blooming stems respectively in 1  $m^2$  plots, and calculating an estimated population density for both rosettes and stems using average clump area, creating two density measures: rosettes per clump area and stems per clump area).

A list of co-occurring taxa, identified to genus (family for Poaceae and Cyperaceae), was compiled for an approximately two-meter radius from the edge of clumps. Other species were generally not present directly within *I. versicolor* clumps. Soil samples of approximately 100 g were collected from near the roots of *I. versicolor* individuals in plastic bags (one per site) and stored at ambient temperatures. Qualitative notes on the locality (broad classifications such as “bog”, “riverbank”, “ditch” as well as notes on disturbances) and observations of anomalous conditions concerning the population were recorded for each site.

For sites where *I. versicolor* was apparently absent, qualitative notes concerning the nature of the habitat were taken to formulate possible explanations for population absence. Soil samples were also taken at each site to measure potentially aberrant pH, electrical conductivity, and soil texture.

During the 2018 field season, emphasis during site visitation was placed on identifying recognized invasive or aggressive species within the suite of co-occurring taxa. “Aggressive” species are defined as species that are native to a region, yet have a tendency to outcompete other native taxa. Selected species are listed in Table 1.

<b>Binomial name</b>	<b>Common name</b>	<b>Potential threat</b>
<i>Typha angustifolia</i> , <i>T. latifolia</i> , <i>T.</i> × <i>glauca</i>	Narrowleaf cattail, broadleaf cattail, hybrid cattail	Native and invasive species tend to outcompete other taxa with environmental changes (Galatowitsch et al., 1999; Drohan et al., 2006; Shih & Fenkelstein, 2008; Olson et al., 2009)
<i>Iris pseudacorus</i>	Yellow flag	Directly competes with native <i>Iris</i> species (Morgan, 2019)
<i>Solanum dulcamara</i>	Bittersweet nightshade	Indicator of invasive species dispersal, anthropogenic influence; noxious weed (Cao & Berent, 2019)
<i>Phragmites australis</i>	Common reed	Similar growth habit, outcompetes shoreline species (Galatowitsch et al., 1999)
<i>Lythrum salicaria</i>	Purple loosestrife	Aggressively colonizes banks, riparian systems (Galatowitsch et al., 1999)
<i>Frangula alnus</i> , <i>Rhamnus cathartica</i>	Glossy buckthorn, common buckthorn	Capitalizes on changes in hydrology and prevents returning to natural state; shades out native species (Miletti et al., 2005)

Table 1. Invasive and aggressive species recorded for sites visited in 2018. Species of *Typha*, *Frangula*, and *Rhamnus* were not differentiated in the field due to their similar proposed effects on *I. versicolor* habitat.

During both field seasons, 49 plant specimens were collected from various sites; of these, 20 were specifically *Iris versicolor*, all containing leaf rosettes and the majority containing flowers or fruits. Collections were marked with TJJ and collection number and cross-referenced with the original herbarium voucher from which locality data were taken, if applicable. The specimens were deposited in the University of Michigan Herbarium.

#### Certainty of site location

Due to the large differences in site specificity on herbarium labels, we wanted to confirm that sites declared “absent” were truly lost, not artifacts of poor location data or new populations mistaken for those represented by herbarium specimens. Qualitative measures of “site certainty” were established on a 1-5 scale, with a score of 5 indicating utmost certainty of the correct location/population located, and a score of 1 indicating an inability to adequately verify site location; any voucher receiving a score of 1, even if supposedly visited, was later removed from the study. Figure 3 shows the distribution of certainty metrics for present and absent sites, and the number of sites removed due to poor location data. When compared using a Welch’s t-test, no significant difference is found between present and absent site certainty (P-value = 0.4356).

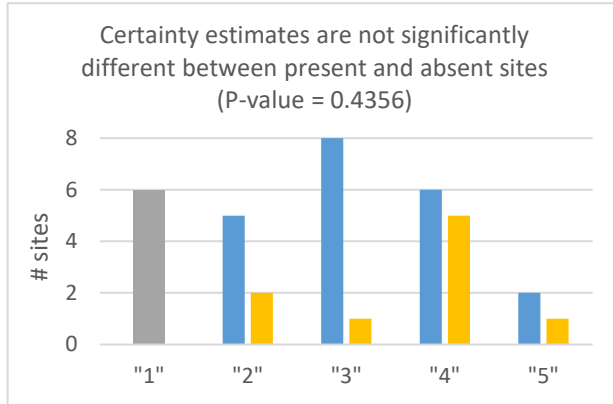


Figure 3. Site “certainty” metrics for present (blue), absent (yellow), and removed (grey) *I. versicolor* research sites. Certainty values are given qualitatively as 1-5, with 5 indicating utmost certainty of site location (i.e., latitude/longitude data) and 1 indicating an inability to determine site location. No significant difference in certainty is found between present and absent sites (P-value = 0.4356).

### Soil testing

From the 100 g soil samples collected, 10 g of unprocessed soil matter were isolated and mixed with 10 mL deionized water. Samples already heavily suspended in solution or essentially liquid were subsampled to 20 mL rather than adding deionized water for a solution. Each sample was then tested for pH and electrical conductivity (the latter measured in milliSiemens, or mS), and assigned a qualitative measure of soil texture via ribbon test (Thien, 1979).

### Proximity to man-made structures/dwellings

Using ArcGIS, distance was measured between data points representing historic populations and man-made structures such as roads (paved and unpaved), buildings, agricultural land, and boat launches. When applicable, proximity to and notes on anticipated impacts of nearby structures were taken on site. In addition to measures from each

disturbance type, the shortest distance from each site to any disturbance was recorded and used to examine effects of general human-mediated disturbances on *I. versicolor* populations.

### Climate data

Yearly temperature averages (degrees Celsius) and precipitation averages (mm) from 1910 to 2017 (sampled regularly at 10 year intervals) were retrieved from the NOAA National Centers for Environmental Information (NOAA, 2019). Data from over 600 stations throughout Michigan were categorized by latitude (for example, data from stations at latitudes 41.0000 through 41.9999 were pooled to represent “41° latitude”) and averaged to create an estimate of average temperature and precipitation for a given latitude (41° to 47°) for a given year.

Years of *I. versicolor* collection were rounded to the nearest year included in the climate dataset (i.e., sites collected 1975-1984 would be rounded to 1980), and values for temperature and precipitation at collection year were subtracted from the values for 2017, at the appropriate latitude, to obtain an average change in temperature and precipitation for each *I. versicolor* site.

### Statistical analyses

Data were imported into R and subjected to Welch’s corrected t-tests for each parameter, using absence and presence of *Iris versicolor* and absence and presence of *Typha* species as test levels. Correlations between variables and linear regressions were calculated to assess patterns in the data.

## Results

Of the 30 sites included in the study, 21 *Iris versicolor* populations were successfully located and analyzed for the aforementioned parameters. Four additional populations of *I. versicolor* that had no associated voucher record were also located, and specimens from these populations were collected and deposited at the UM Herbarium. These “extra” sites are appended to the original 30 sites, for a total of 25 present sites and 9 absent sites used in subsequent analyses (Table 2). A map of the located sites and a graphic of the relative proportions of each site type are given in Figure 4. Absent site occurrence trended toward a slightly lower latitude than present sites, on average (44.3678° N versus 45.2555° N; P-value = 0.0822).

The invasive taxa emphasized in this study were found at 14 of the extant populations, and 8 of the absent (22/34 sites total). Extant populations co-occurred with zero to two invasive taxa, whereas sites of absent populations included up to five invasive taxa (Figure 5a). Invasive richness appears to correlate negatively with latitude (Table S1) and exhibits this trend most strongly at absent sites (Figure 5c). The vast majority of sites with invasive taxa were co-occurring at least with *Typha*, with minimal occurrences of other invasive taxa (Figure 5b). *Typha* occurred at 8 of 9 (89%) sites where *I. versicolor* was deemed absent versus 11 of 25 (44%) for present and extra sites (P-value = 0.0069).

Distances of *I. versicolor* sites from human-mediated disturbances were most abundant for distances from paved and unpaved roads and buildings. The disturbance type that was most often the shortest distance to *I. versicolor* sites was unpaved (dirt) roads (positive correlation shown in Table S1). For absent sites, shortest distance to human disturbance appeared to decrease sharply with latitude; however, upon adjusting for outliers (see Discussion), shortest distance to human disturbance increased with increasing latitude (Figure 6a and b). Richness of invasive taxa decreased exponentially with increasing distance from invasive taxa (Figure 6c). Further analyses revealed that sites with *Typha* co-occurrence have significantly shorter distances to human disturbances (Figure 6d; P-value = 0.0464).

Shortest distance to human disturbance was found to correlate negatively with pH of *I. versicolor* sites – i.e., pH appeared to increase in *I. versicolor* sites closer to human disturbances (Table S2, Figure 7a). When examining this trend with *Typha* co-occurrence, sites with *Typha* had significantly higher pH (P-value = 0.001561, Figure 7b). Further analyses of this relationship found that sites with *Typha* co-occurrence also had significantly higher EC values (P-value = 0.04562), and lower values for latitude (P-value = 0.01424). The observed trends for these values for *I. versicolor* and *Typha* presence/absence are compared in Figure 8.

Total population area, the main metric of population “size” for this study, was found to be highly variable among *I. versicolor* populations, with values ranging from less than 1 m<sup>2</sup> to over 350 m<sup>2</sup>. Few parameters had meaningful correlations, although a weak negative trend was observed with both soil pH and EC (Table S2). When observed in relation to *Typha* co-occurrence, a strong correlation between *Typha* co-occurrence, increasing pH, and decreasing population size was observed (P-value = 0.0268; Figure 9a). No significant trend was observed for soil EC (Figure 9b). To confirm whether the observed trend was a function of *Typha* co-occurrence or distance to human disturbance, population area was examined in relation to distance to human disturbance; no significant difference between sites with and without *Typha* co-occurrence was observed (P-value = 0.4323; Figure 9c).

Soil textures were classified into 11 types (using methodology described in Methods), plus “decaying organic matter” when excessive amounts of humus, unidentifiable “muck”, or animal feces were present at a site (Figure 10). Most *I. versicolor* sites identified as present were located in primarily loamy soils, while most sites recorded as absent possessed sandy soils.

To examine trends in average temperature and precipitation per latitude bracket, as well as the average for the entire state, we plotted the average temperature and precipitation per latitude once every ten years over the past 100 years (Figure 11). Average temperature shows a steady increase across all latitudes over time,

with no single latitude showing a significant deviation from the mean. Average temperature for latitudes 41, 42, and 43° N have increased from 9.26, 8.46, and 7.93° C to 10.21, 9.49, and 9.12° C, respectively; the average annual temperature at 43°N for 2017 almost exceeds that of 41°N in 1910. Average precipitation for the entire state shows an increasing trend over time. There appears to be more variation across latitudes, but again, no single latitude shows a trend with a significant deviation from the mean.

To examine trends in population presence/absence over time, voucher age was compared with change in average temperature and precipitation at site latitudes between collection year and 2017 (Figure 12a and b). As expected, average changes in temperature and precipitation decreased over time across all sites, with a significant decline for temperature (P-value = 0.0234). No significant differences were observed between present and absent populations for average change in temperature or precipitation (P-values = 0.3548 and 0.3564, respectively). Year of collection was plotted against latitude (Figure 12c), and specimens that were collected after that latitude had experienced an average annual temperature greater than 8°C (average annual temperature at the southern margin of *I. versicolor*'s range, 43°N, in 1910) were indicated. This shows that the most recent *I. versicolor* collections up to 45°N latitude have experienced average annual temperatures in excess of *I. versicolor*'s southern margin in 1910.



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<i>Sites</i>	<i>P/A</i>	<i>TA</i>	<i>C</i>	<i>ACA</i>	<i>R/CA</i>	<i>S/CA</i>	<i>pH</i>	<i>EC</i>	<i>ST</i>	<i>Lat</i>
17	0	0.00	0.00	0.00	0.00	0.00	4.85	0.01	9	46.0431
22	0	0.00	0.00	0.00	0.00	0.00	7.71	0.17	11	45.7711
23	0	0.00	0.00	0.00	0.00	0.00	6.94	0.18	7	44.1179
57	0	0.00	0.00	0.00	0.00	0.00	7.73	1.43	*	45.0069
66	0	0.00	0.00	0.00	0.00	0.00	6.94	0.41	11*	44.3118
75	0	0.00	0.00	0.00	0.00	0.00	8.22	0.15	8	43.1465
76	0	0.00	0.00	0.00	0.00	0.00	7.32	0.20	5	42.1274
81	0	0.00	0.00	0.00	0.00	0.00	7.11	0.18	4	43.5942
84	0	0.00	0.00	0.00	0.00	0.00	7.41	0.42	10*	45.1905
1	1	242.01	6.00	1.39	12.20	1.44	6.81	0.13	6	44.5236
3	1	11.61	1.00	11.61	3.88	0.00	6.24	0.01	8	46.1802
5	1	232.26	6.00	0.42	83.71	14.35	6.15	0.51	3	45.1972
6	1	304.80	12.00	0.14	14.35	7.18	7.15	0.25	3	45.0810
9	1	34.84	3.00	3.25	15.38	1.54	6.16	0.22	2	45.6099
10	1	0.84	1.00	0.84	23.92	11.96	7.45	0.41	6	45.4406
12	1	9.29	3.00	0.19	32.29	5.38	5.44	0.01	8	46.3391
21	1	1.95	1.00	1.95	15.38	0.00	6.49	0.34	6	45.3364
27	1	97.55	6.00	0.09	64.59	0.00	7.14	0.07	8	44.6762
35	1	0.09	1.00	0.09	200.00	44.44	8.01	0.24	8	44.4715
55	1	62.50	6.00	2.22	50.00	25.00	7.25	0.13	9	44.0340
56	1	242.01	1.00	0.09	43.06	0.00	5.49	0.03	2	44.5021
58	1	45.00	4.00	2.28	20.00	5.00	6.53	0.12	7	43.6199
60	1	338.82	10.00	2.23	4.04	1.35	6.88	0.19	2	44.4099
65	1	0.98	1.00	0.98	25.63	7.18	7.32	0.03	2	45.4039
68	1	9.29	1.00	9.29	23.55	6.73	6.86	0.15	5	45.9746
70	1	2.32	1.00	2.32	2.15	1.29	7.40	0.42	8	45.9534
72	1	27.87	2.00	4.55	8.79	0.00	6.47	0.00	8	45.9701
73	1	232.26	15.00	0.37	13.46	2.69	5.64	0.00	8	46.3443
74	1	1.86	1.00	1.86	5.92	2.69	7.16	0.80	9	46.4179
79	1	8.25	1.00	8.25	12.00	2.00	7.49	0.29	3	43.1104
**014	1	1.30	1.00	1.30	3.84	2.31	7.11	0.62	2	45.3556
**015	1	0.37	2.00	0.14	86.11	14.35	8.33	0.11	1	44.4923
**016	1	83.61	8.00	2.97	8.41	2.35	6.25	0.18	7	46.4660
**019	1	69.68	1.00	69.68	29.90	4.48	6.76	0.15	6	46.4765
<i>Sites</i>	<i>D/U</i>	<i>D/P</i>	<i>D/B</i>	<i>D/AF</i>	<i>D/BL</i>	<i>SD</i>	<i>Age</i>	<i>YC</i>	<i>Cert</i>	
17	0.039	1.220	1.280	—	—	0.039	41	1976	2	
22	0.200	0.610	0.093	—	—	0.093	70	1947	4	
23	0.100	0.001	0.160	—	—	0.001	34	1983	4	
57	0.370	0.006	0.070	—	—	0.006	61	1956	2	
66	0.002	1.000	0.830	—	—	0.002	44	1973	5	
75	0.032	0.070	0.580	—	—	0.032	10	2007	3	
76	0.880	1.300	0.815	—	—	0.815	8	2009	4	
81	0.640	0.790	0.347	—	—	0.347	90	1927	4	
84	0.003	0.900	0.810	—	—	0.003	21	1996	4	
1	0.004	1.370	1.400	—	—	0.004	80	1937	4	
3	0.600	2.310	0.138	—	—	0.138	82	1935	3	
5	0.037	1.640	0.110	—	—	0.037	69	1948	3	
6	0.008	2.410	0.560	—	—	0.008	32	1985	4	
9	0.167	6.600	3.060	3.630	—	0.167	63	1954	3	
10	0.004	0.390	0.030	—	0.004	0.004	103	1914	2	
12	0.570	2.180	0.533	—	—	0.533	49	1968	4	
21	0.018	0.200	0.200	—	—	0.018	70	1947	4	
27	0.036	0.520	0.550	—	—	0.036	15	2002	4	
35	—	0.002	—	—	0.002	0.002	78	1939	3	
55	1.150	0.025	1.020	—	—	0.025	88	1929	4	
56	0.142	1.730	1.500	—	—	0.142	66	1951	3	
58	0.009	0.890	0.070	—	—	0.009	19	1998	3	
60	0.010	2.740	1.000	—	—	0.010	8	2009	3	
65	0.015	1.630	1.400	—	—	0.015	63	1954	3	
68	0.040	0.140	0.027	—	—	0.027	78	1939	5	
70	0.290	0.089	0.160	—	—	0.089	75	1942	2	
72	0.024	0.600	0.630	—	—	0.024	35	1982	2	
73	0.020	0.350	2.620	—	—	0.020	61	1956	2	
74	0.002	1.320	9.370	—	—	0.002	45	1972	2	
79	0.004	0.460	0.070	—	—	0.004	79	1938	5	
**014	—	0.007	0.260	—	—	0.007	—	2017	—	
**015	0.005	1.020	0.090	—	—	0.005	—	2017	—	
**016	0.072	0.080	0.150	—	—	0.072	—	2017	—	
**019	0.008	0.100	1.220	—	—	0.008	—	2017	—	

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Sites	IR	T	IP	SD	PA	LS	FR	AvgT	AvgP
17	0	0	0	0	0	0	0	1.79	10.61
22	1	1	0	0	0	0	0	3.57	7.90
23	1	1	0	0	0	0	0	3.38	12.15
57	1	1	0	0	0	0	0	1.92	4.97
66	1	1	0	0	0	0	0	1.60	10.34
75	1	1	0	0	0	0	0	0.08	9.37
76	4	1	0	1	1	1	1	-0.20	5.98
81	3	1	0	0	1	1	1	0.97	17.22
84	3	1	0	1	0	1	0	0.48	12.87
1	1	1	0	0	0	0	0	2.92	7.37
3	1	0	1	0	0	0	0	1.36	7.85
5	1	1	0	0	0	0	0	3.57	7.90
6	1	1	0	0	0	0	0	-0.49	7.16
9	0	0	0	0	0	0	0	3.57	7.90
10	1	1	0	0	0	0	0	1.59	14.65
12	0	0	0	0	0	0	0	1.02	8.01
21	0	0	0	0	0	0	0	3.57	7.90
27	0	0	0	0	0	0	0	0.60	10.45
35	1	1	0	0	0	0	0	2.92	7.37
55	1	0	1	0	0	0	0	1.84	18.68
56	0	0	0	0	0	0	0	3.09	6.51
58	2	1	0	1	0	0	0	1.69	2.78
60	0	0	0	0	0	0	0	-1.09	12.06
65	0	0	0	0	0	0	0	3.57	7.90
68	1	1	0	0	0	0	0	2.53	7.30
70	0	0	0	0	0	0	0	2.53	7.30
72	0	0	0	0	0	0	0	2.27	13.31
73	0	0	0	0	0	0	0	1.02	8.01
74	1	1	0	0	0	0	0	1.02	8.01
79	2	1	0	1	0	0	0	3.30	5.80
**014	1	0	1	0	0	0	0	—	—
**015	1	1	0	0	0	0	0	—	—
**016	0	0	0	0	0	0	0	—	—
**019	1	1	0	0	0	0	0	—	—

Table 2. Raw data for each site. P/A = presence/absence, TA = total area, C = clumps, ACA = average clump area, R/CA = rosettes per clump area, S/CA = stems per clump area, pH = soil pH, EC = soil electrical conductivity, ST = soil texture, Lat = latitude, D/U = distance from unpaved road, D/P = distance from paved road, D/B = distance from building, D/AF = distance from agricultural field, D/BL = distance from boat launch, SD = shortest distance, Age = voucher age, YC = year collected, Cert = certainty, IR = richness of invasive taxa, T = *Typha* species present, IP = *Iris pseudacorus*, SD = *Solanum dulcamara*, PA = *Phragmites australis*, LS = *Lythrum salicaria*, FR = *Frangula* and *Rhamnus* species present, AvgT = average change in temperature, and AvgP = average change in precipitation. Soil texture values range from 1-11, where 1 = clay, 2 = clay loam, 3 = silty clay loam, 4 = silty clay, 5 = silty loam, 6 = loam, 7 = sandy clay loam, 8 = sandy loam, 9 = loamy sand, 10 = sand, and 11 = sand and rock. \* values indicate “decaying organic matter” as a substantial component of soil substrate. Presence/absence values of 0 represent absent populations, and values of 1 represent present populations. Site values in the format “\*\*0##” are “extra” sites.

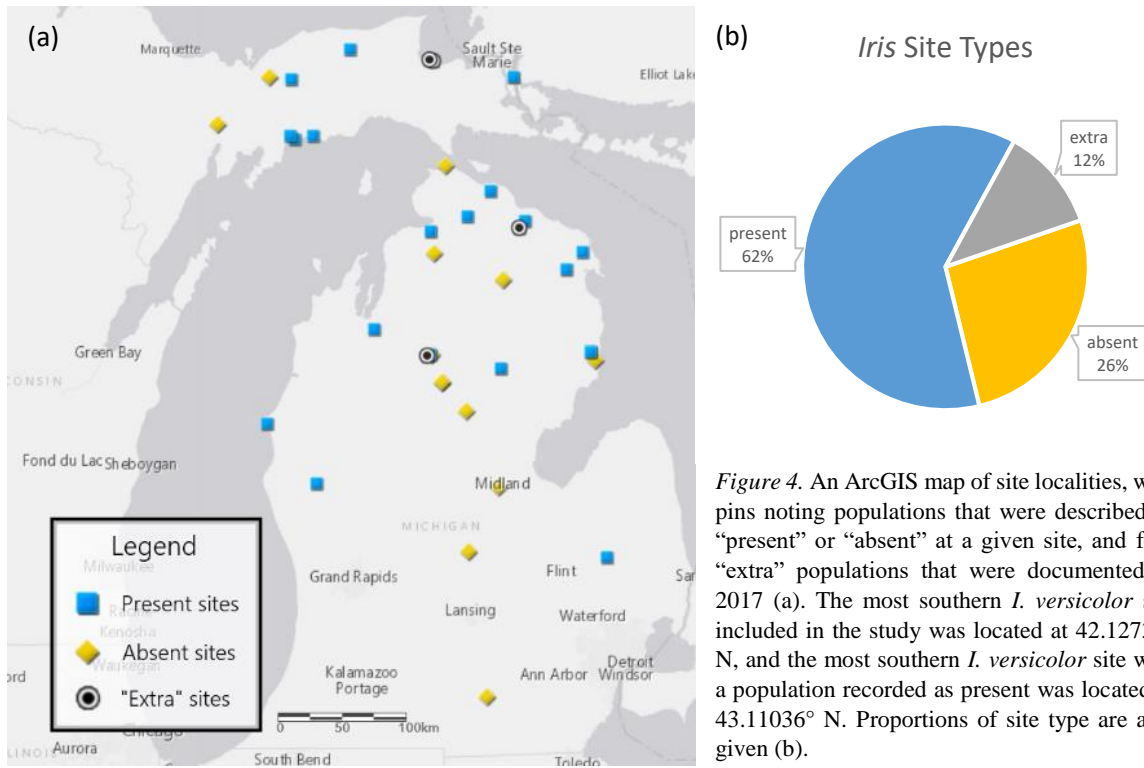


Figure 4. An ArcGIS map of site localities, with pins noting populations that were described as “present” or “absent” at a given site, and four “extra” populations that were documented in 2017 (a). The most southern *I. versicolor* site included in the study was located at 42.12738° N, and the most southern *I. versicolor* site with a population recorded as present was located at 43.11036° N. Proportions of site type are also given (b).

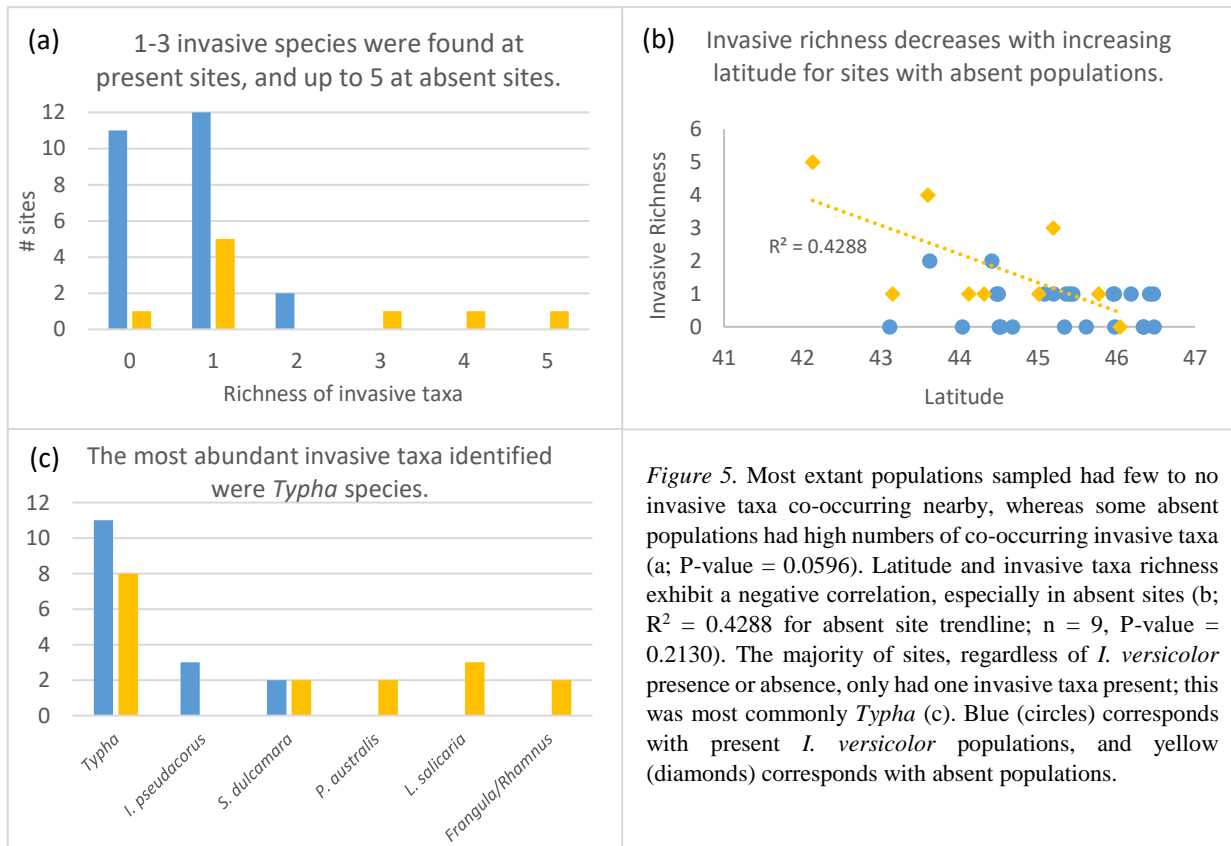


Figure 5. Most extant populations sampled had few to no invasive taxa co-occurring nearby, whereas some absent populations had high numbers of co-occurring invasive taxa (a; P-value = 0.0596). Latitude and invasive taxa richness exhibit a negative correlation, especially in absent sites (b;  $R^2 = 0.4288$  for absent site trendline;  $n = 9$ , P-value = 0.2130). The majority of sites, regardless of *I. versicolor* presence or absence, only had one invasive taxa present; this was most commonly *Typha* (c). Blue (circles) corresponds with present *I. versicolor* populations, and yellow (diamonds) corresponds with absent populations.

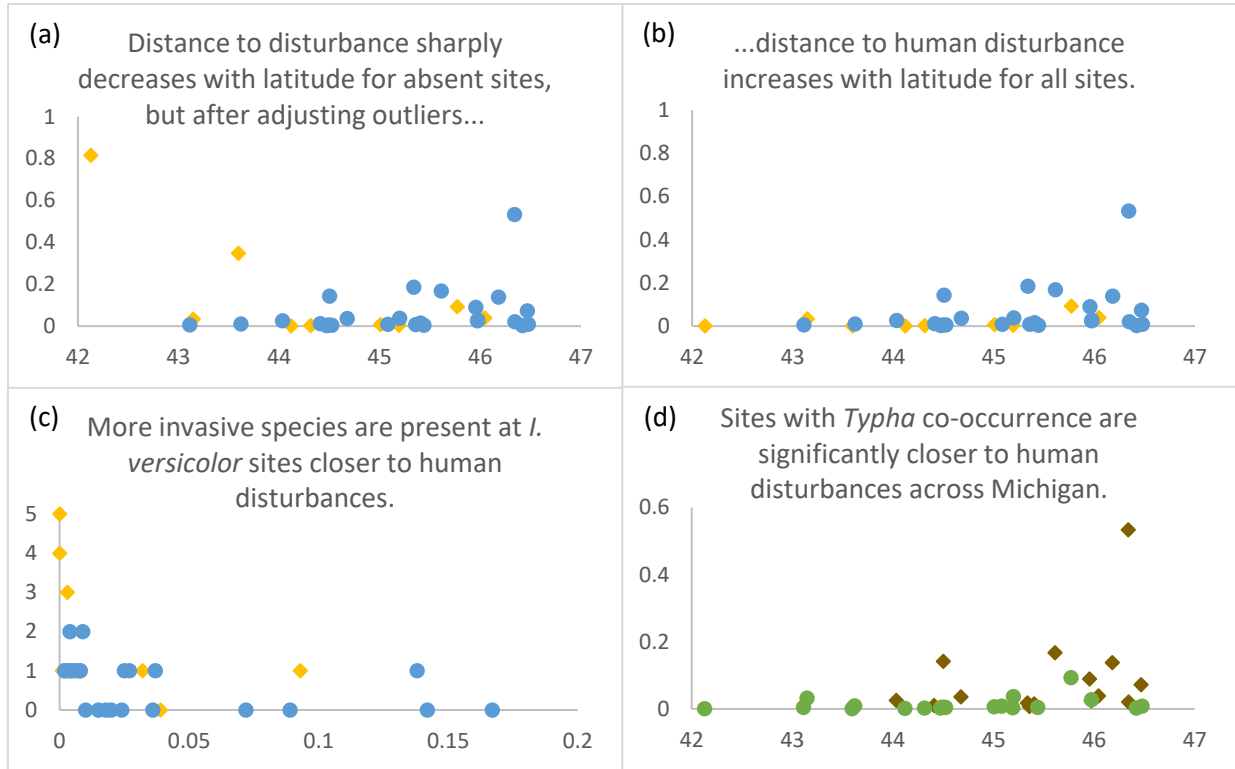


Figure 6. Shortest distance (km) of *I. versicolor* sites from human disturbances shows interesting trends. Initial analyses show absent sites are farthest from human disturbance at low latitudes (a), but after adjusting outliers (see Discussion), distance to human disturbance increases with latitude for all sites (b). There appears to be an exponential relationship between distance to human disturbance and number of invasive taxa (c). Further analysis reveals that sites with *Typha* co-occurrence are significantly closer to human disturbances than sites without *Typha* (d; P-value = 0.0464). For a, b, and c, blue (circles) corresponds with present *I. versicolor* populations, and yellow (diamonds) corresponds with absent populations. For d, green (circles) corresponds with *Typha* co-occurrence, and brown (diamonds) corresponds with no *Typha* co-occurrence.

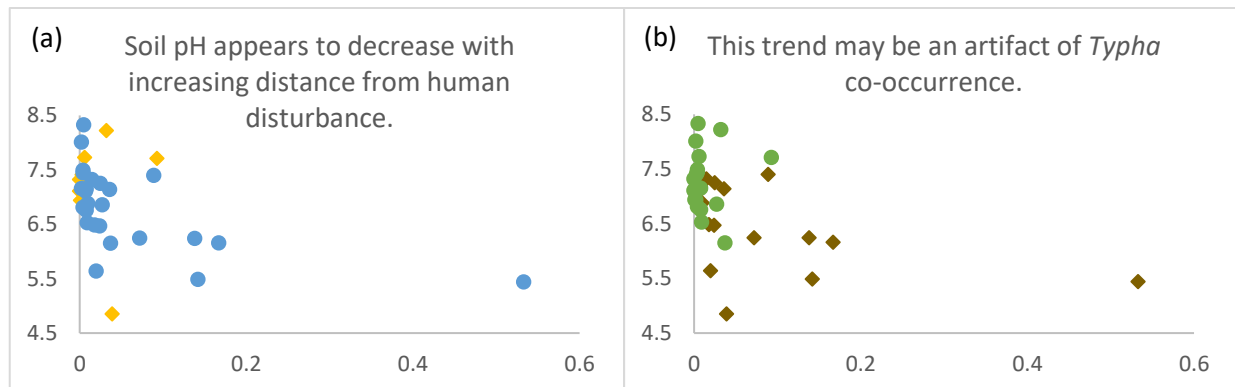


Figure 7. Relationships between shortest distance to human disturbance and soil pH. Soil pH appears to decrease as sites are located farther away from human disturbance (a). When looking at the distribution of sites with *Typha* co-occurrence, it was found that sites with *Typha* have significantly higher pH (b, P-value = 0.0016). For a, blue (circles) corresponds with present *I. versicolor* populations, and yellow (diamonds) corresponds with absent populations. For b, green (circles) corresponds with *Typha* co-occurrence, and brown (diamonds) corresponds with no *Typha* co-occurrence.

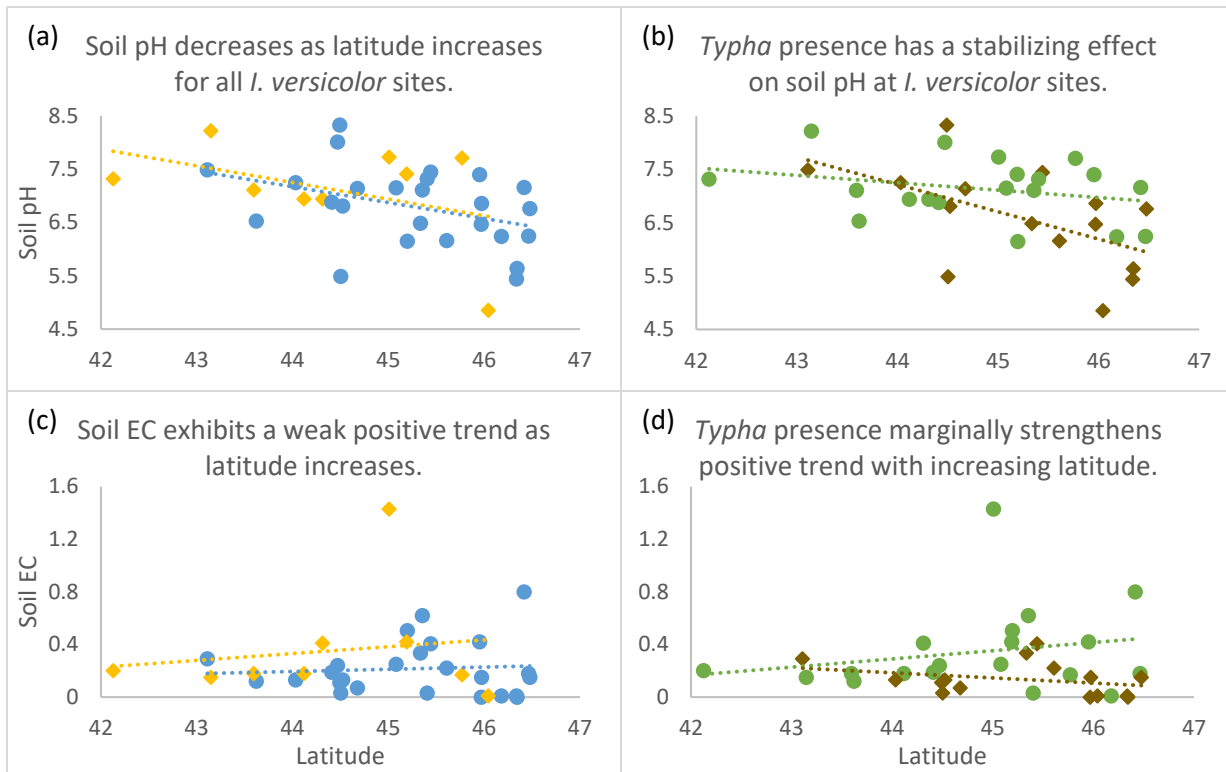


Figure 8. A comparison of trends for *I. versicolor* presence/absence and *Typha* co-occurrence at *I. versicolor* sites. Trends show pH consistently decreasing with increasing latitude, though co-occurrence with *Typha* appears to stabilize pH across latitude (a and b). Soil electrical conductivity (EC) appears to increase weakly with increasing latitude, and *Typha* co-occurrence marginally increases the trend (c and d). Blue (circles) and yellow (diamonds) show *I. versicolor* presence/absence, respectively; green (circles) and brown (diamonds) show *Typha* co-occurring or not at *I. versicolor* sites.

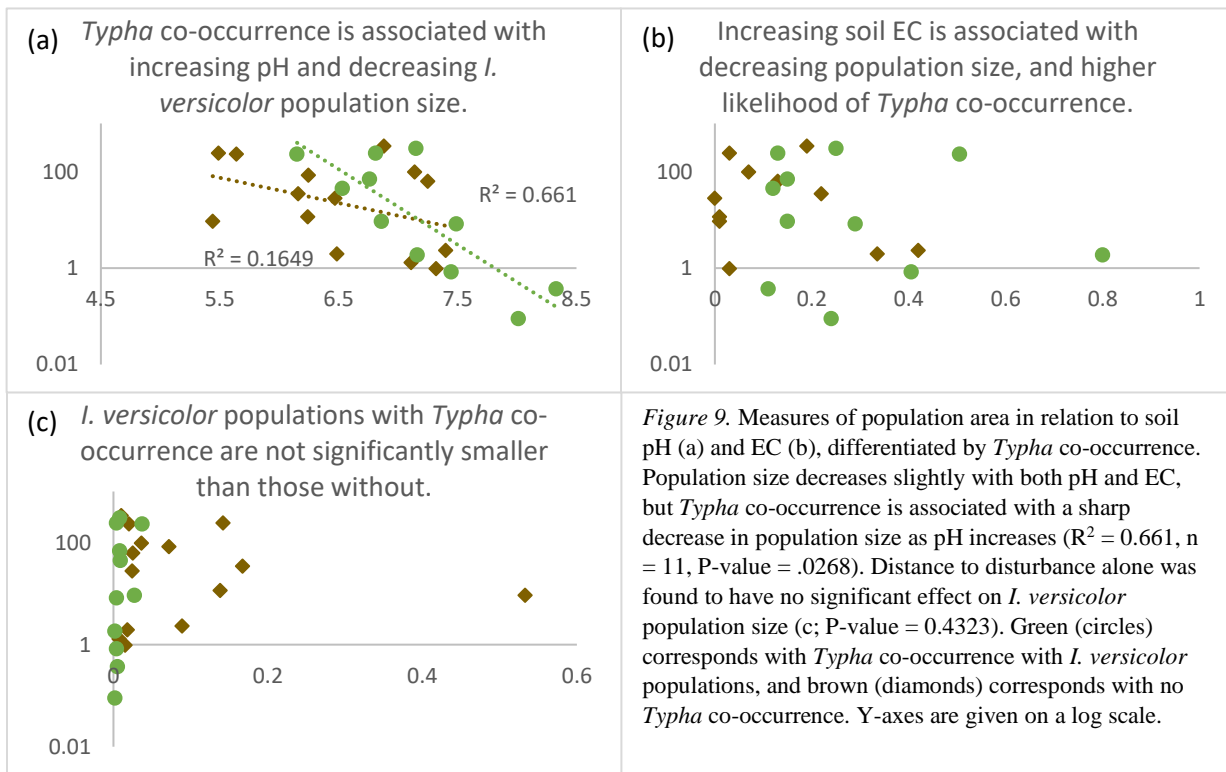


Figure 9. Measures of population area in relation to soil pH (a) and EC (b), differentiated by *Typha* co-occurrence. Population size decreases slightly with both pH and EC, but *Typha* co-occurrence is associated with a sharp decrease in population size as pH increases ( $R^2 = 0.661$ ,  $n = 11$ ,  $P$ -value = .0268). Distance to disturbance alone was found to have no significant effect on *I. versicolor* population size (c;  $P$ -value = 0.4323). Green (circles) corresponds with *Typha* co-occurrence with *I. versicolor* populations, and brown (diamonds) corresponds with no *Typha* co-occurrence. Y-axes are given on a log scale.

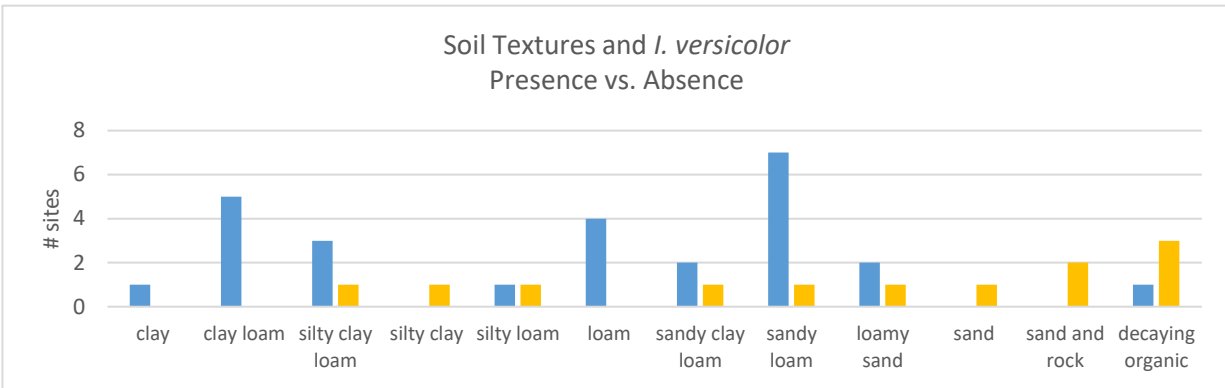


Figure 10. Soil texture types against number of present and absent sites. Present sites are indicated by blue bars, and absent sites are indicated by yellow bars. The majority of present sites had soil with loamy character, while most absent sites had silty or sandy character. “Decaying organic” refers to soils mainly comprised of wet humus material or manure.

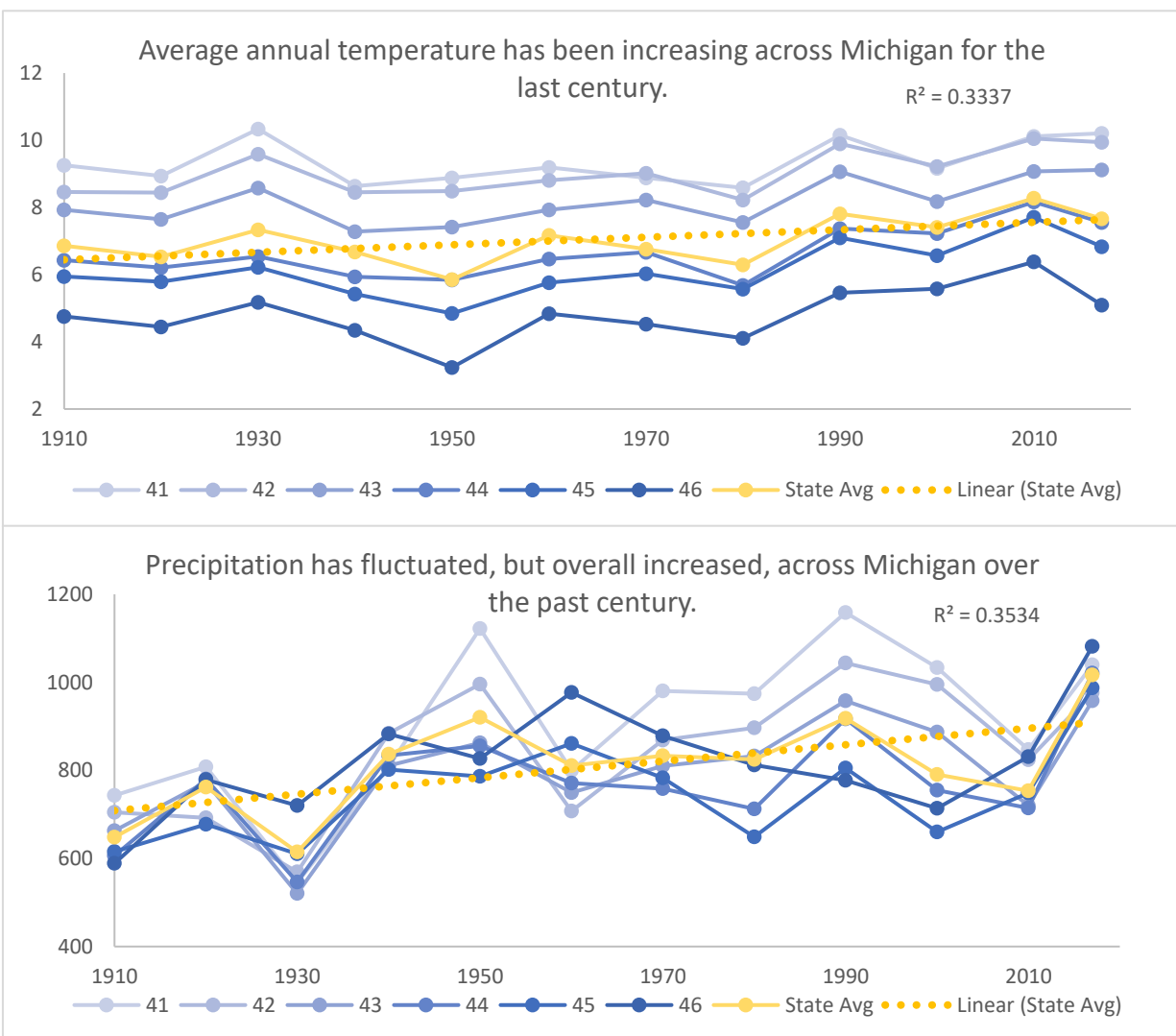
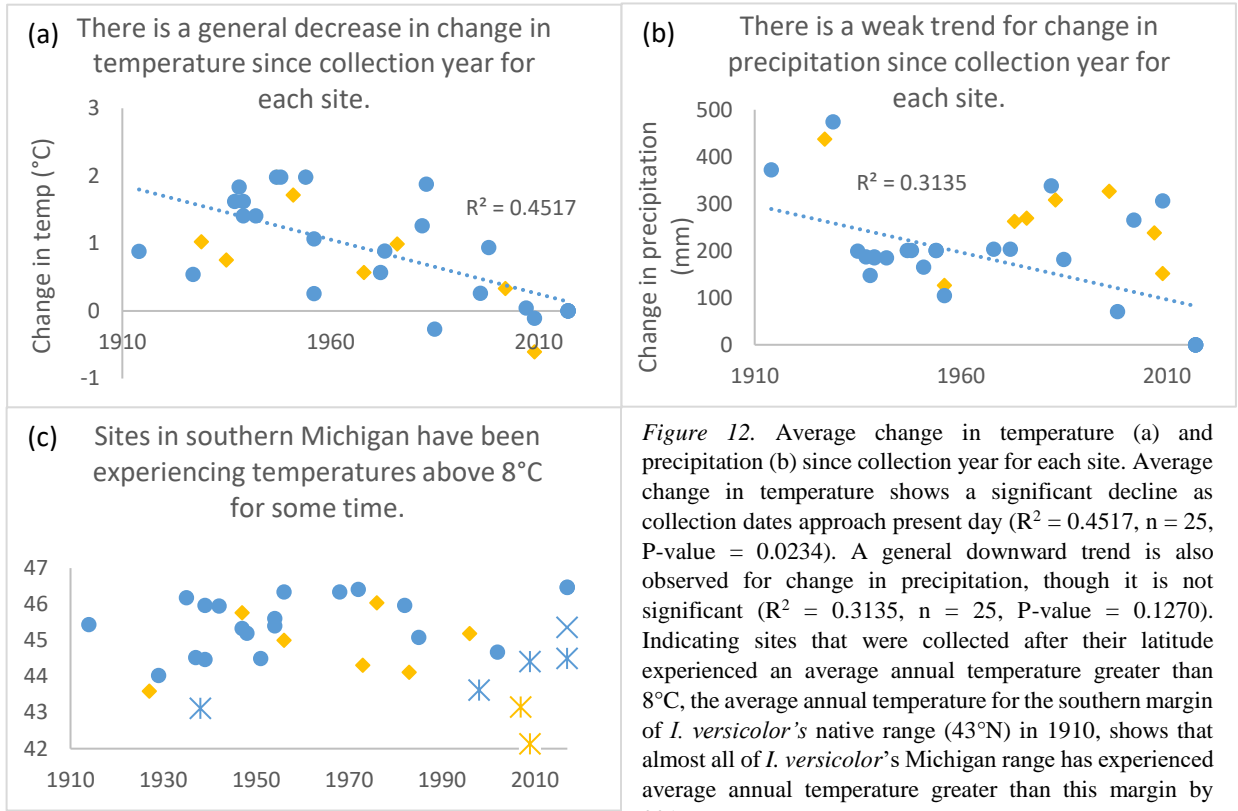


Figure 11. Average temperature (°C) and precipitation (mm) for latitudes across Michigan, every ten years from 1910 to 2017. Average temperatures have steadily increased throughout the state over the past century. Average precipitation has generally increased, but with more variation than average temperature. Average temperature for latitudes 41, 42, and 43° N have increased from 9.26, 8.46, and 7.93° C to 10.21, 9.49, and 9.12° C, respectively.



## Discussion

The most interesting results we have found are in relation to: 1) a latitudinal gradient of *I. versicolor* presence/absence, 2) the effect of invasive species on *I. versicolor* presence/absence, and 3) the effect of *Typha* co-occurrence on soil pH and *I. versicolor* population size. Implications of soil texture are also discussed, as well as study limitations and future directions.

### Latitude and *Iris versicolor* presence/absence

Statistical t-tests showed a trend of more *Iris versicolor* populations being absent at southern sites on average (44.3678° N versus 45.2555° N; P-value = 0.0822). While not statistically significant, this trend may indicate potential effects on *I. versicolor* populations at the southern edge of its range.

Patterns of *I. versicolor* absence at southern latitudes may be linked with habitat destruction through degradation of wetlands, competition with invasive or newly aggressive species, or changes in temperature or precipitation associated with climate change. At least the latter two of these potential effects are most exacerbated at the southern edge of *I. versicolor*'s range (Figures 5, 11, 12). Our data most support the invasion hypothesis, with more invasive species being identified both at absent and at lower latitude sites (Figure 5c, P-value = 0.0596). However, invasive species competition may be facilitated by warming throughout Michigan, with average annual temperatures increasing by as much as 2.7° C over the past century (42° N; Figure 11). Warming temperatures may also reduce the competitive ability of *I. versicolor*, leading to a higher susceptibility to being outcompeted at southern sites. This competition may occur between not only *I. versicolor* and invasive species, but also more southern-ranged native species that have co-occurred with *I. versicolor* for years or even decades. As an indication of this, we can further examine the temperature data in Figures 11 and 12.

The native range of *I. versicolor* in Michigan reaches as far south as Newaygo and Sanilac Counties, whose southern boundaries are at 43°N (Reznicek et al., 2011). Historic data for latitudes 41, 42, and 43° N show average temperature increases from 9.26, 8.46, and 7.93°C to 10.21, 9.49, and 9.12°C, respectively; the average annual temperature for 43°N latitude in 2017 has almost reached that of 41°N latitude in 1910. Furthermore, we compared changes in average annual temperature at each latitude with the recorded annual temperature for 43°N in 1910 (about 8°C; Figure 12c). By 2017, latitudes up to 45°N had experienced average annual temperatures above 8°C. Assuming climate (and especially temperature) is a crucial factor of delimiting species ranges, we suggest that the range of *I. versicolor* is shifting northward as southern populations become less fit and die out from stress or competition. This trend is observed in other plant and animal species in various regions (Lesica & McCune, 2004; Kelly & Goulden, 2008; Chen et al., 2011). Under this assumption, new *I. versicolor* populations should also become established at more northern latitudes than previously recorded, though the ability of *I. versicolor* and other plants to establish at the same rate of southern range die-off is contested (DiMento & Doughman, 2014).

Evidence is also found for the hypothesis of habitat destruction via human construction of roads and buildings. Distance to unpaved and paved roads show little to no correlation with latitude, but distances to buildings and shortest overall distance to disturbance have notable correlations (Tables S1 and S2). The two southernmost sites – both with absent *I. versicolor* populations – have the first and third highest “shortest distance” values recorded for this study, meaning they were located farthest away from the human disturbances we considered (Table 2). However, these sites were also located within nature reserves undergoing processes of invasive species removal; thus, it could be argued that these sites have the closest proximity to human disturbances of all sites in this study. With this revision, site distance from human disturbance increases slightly with latitude, and sites with *Typha* co-occurrence are significantly closer to human disturbances (Figure 6, P-value = 0.0464). Hence, disturbance may also lead to increased vulnerability at *I. versicolor* sites, especially more southern sites. This triple-threat for southern *I. versicolor* populations – increased proximity to human disturbances, average annual temperatures reaching



unfavorable levels, and more co-occurrence with invasive species – may contribute to *I. versicolor* population disappearance.

Despite these hypotheses, there is the potential of systematic error within our data. As shown in Figure 4, study sites were not evenly distributed throughout the state, especially in the southern *I. versicolor* range. The average of the highest and lowest latitudes for all sites (46.47647° N and 42.12738° N respectively) is 44.3019° N, nearly a full degree of latitude lower than the average latitude of all sites, 45.0205° N. Furthermore, when using these averages to compare incidence of *I. versicolor* sites at higher and lower latitudes, 7 sites were located below 44.3019° N and 15 were located below 45.0205° N. Thus, while the observed trend in site latitude is potentially interesting for examining *I. versicolor*'s response to latitude-dependent variables, such as warming climate, the paucity of sampling especially in *I. versicolor*'s southern range prevents us from claiming with certainty that a climate or human disturbance effect is present along a latitudinal gradient. Increasing the sample size of the study, especially in the lower portion of *I. versicolor*'s range in Michigan, may confirm or reject the observation of latitudinal presence/absence.

#### *Typha* impact on *Iris versicolor* presence/absence and population size

The most common invasive species at each site were members of the genus *Typha* (Figure 5). *Typha* presence was recorded for every absent site except the northernmost one, and was found to correlate highly with site latitude for all site types, but also with soil pH and EC (Table S1; Figures 7 & 8). The correlations with site absence and latitude support our hypothesis that southern *I. versicolor* sites are more vulnerable to being outcompeted, though it is difficult to determine the strength of effect of climate variables. Human activities may facilitate *Typha* dispersal and aggression across all of Michigan, whether through intentional planting of *Typha* to prevent fertilizer run-off and aid in wastewater treatment (Hammer, 1992; Nilratnisakorn et al., 2009; Prellwitz & Thompson, 2014), or through unintentional disturbances that can give *Typha* an edge on other native species (Shih & Fenkelstein, 2008; Olson et al., 2009, Albert & Minc, 2014).

*Typha* co-occurrence is shown to have a stabilizing effect on soil pH and EC across latitudes, showing less fluctuation with increasing latitude than sites without *Typha* (Figure 8). The correlations with soil properties could be due to some property of *Typha* in riparian systems, where *Typha* is able to regulate soil pH and EC; this idea underlies the use of *Typha* in wastewater treatment plots, to “clean” water systems (Nilratnisakorn et al., 2009). However, the observed trends could also signify a difference in fundamental niche for *I. versicolor* and *Typha* species, where *I. versicolor* is better adapted to soils with lower levels of pH than *Typha* species. *I. versicolor* has been shown to adapt to acidic soils through thickening its rhizome, supporting this claim (Gates & Erickson, 1924). This would indicate that changes in pH are not driven by *Typha* co-occurrence, but by some other factor, like proximity to a human disturbance – but our data do not show a strong relationship between pH and proximity to human disturbance when *Typha* is not included (Figure 7). A combination of these hypotheses may apply, in which *Typha* is most competitive at pH values near 7, and is able to somewhat regulate pH to achieve these levels, creating a more ideal habitat for itself in the process. This may contribute to the aggressive nature of *Typha* species in their natural habitats (Shih & Fenkelstein, 2008; Olson et al., 2009; Albert & Minc, 2014).

Furthermore, we have uncovered a significant relationship between *Typha* co-occurrence, increasing pH, and decreasing *I. versicolor* population size (Figure 9a). It appears that increasing the alkalinity of soils alone has no significant effect on *I. versicolor* population size (P-value = 0.5732), but increasing pH and *Typha* co-occurrence leads to major decreases in *I. versicolor* population size (P-value = 0.0268). This does not appear to be an artifact of distance to human disturbance, as there is no significant difference in population size between sites with *Typha* co-occurrence and those without (Figure 9c, P-value = 0.9792).

Combining these evidences, we may conclude with reasonable certainty that competition with *Typha* species is a considerable threat to the population size and overall abundance of *I. versicolor* in Michigan. Future studies that differentiate between various *Typha* species in Michigan (i.e., native species *T. latifolia*,

introduced species *T. angustifolia*, and invasive hybrid *T. ×glauca*) may uncover more nuanced relationships between *Typha* species and *I. versicolor* and other native riparian species.

#### Other invasive species

Other invasive species were not emphasized in the results due to the low frequency of recorded occurrence of each invasive species per site. Attempting to draw conclusions from population sizes of less than four occurrences is not justified, especially when species occurred only at present (*Iris pseudacorus*) or only at absent (*Phragmites australis*, *Lythrum salicaria*, *Frangula alnus/Rhamnus cathartica*) sites.

Low frequency of recorded invasive species per site may be due to methodological error since these species were not emphasized in co-occurring taxa identification until the second research period, summer 2018. Because the second research period also focused on sites at lower latitudes, the observed trend of invasive species richness with lower latitude may be an artifact of the sampling rather than a real trend. Nonetheless, interesting notes are made here about invasive taxa patterns near *I. versicolor* sites.

*Iris pseudacorus*, the yellow flag, is an invasive *Iris* introduced to the United States as an ornamental that promptly escaped cultivation. It is classified as an invasive weed in 12 states in the US, including Michigan (Morgan, 2019). Its habit and preferred habitat are nearly identical to that of *I. versicolor*, and as such it would be expected to outcompete the native species; however, *I. pseudacorus* was recorded at only three *I. versicolor* sites. Furthermore, these sites all had present *I. versicolor* populations. The two species appeared to co-occur along rivers and lakeshores rather than directly compete for habitat. None of the three voucher specimens from the *I. versicolor* sites mentioned presence of *I. pseudacorus* at time of collection, so it is unknown how long these populations have co-occurred; monitoring of these sites in years to come may be necessary to assess the extent of competitive interaction that may exist between these species.

*Frangula alnus* and *Rhamnus cathartica*, glossy buckthorn and common buckthorn respectively, are members of the Rhamnaceae and notorious invaders of the Great Lakes Region (Michigan Natural Features Inventory, 2012; Stuartevant, 2019). These shrubs leaf out early and hold their leaves until late in the season, obscuring light from native understory species and decreasing native plant diversity. These plants have also been associated with altering nutrient cycling and facilitating changes in soil hydrology, draining wetlands and preventing recolonization of riparian species (Miletti et al., 2005). Two sites had recorded occurrences of *Frangula* or *Rhamnus*, both of which were located in preservation areas: the Chippewa Nature Center in Midland County, and the MacCreedy Reserve in Jackson County. Both nature areas had signs detailing buckthorn removal projects and the potential ecological threats these taxa present, and *I. versicolor* was absent in both areas. In fact, the two sites with the highest invasive taxa richness were the two sites designated as public nature areas dedicated to native plant conservation. This great irony may indicate that despite our best efforts, invasive species dispersal is greatest where human traffic is greatest.

*Phragmites australis*, common reed, and *Lythrum salicaria*, purple loosestrife, were both recorded as present at the two nature reserve sites previously mentioned, and *L. salicaria* was also found at a disturbed site in Petoskey County where no *I. versicolor* was identified. Since neither of these taxa were found frequently nor in isolation from other invasive taxa, it is difficult to surmise the strength of their relative impacts on *I. versicolor* population presence/absence.

*Solanum dulcamara*, bittersweet nightshade, is a climbing herbaceous plant in the Solanaceae. It is not a species that would appear to readily compete with *I. versicolor*, since it is not strictly riparian nor would prefer to climb *I. versicolor* and potentially shade or constrict the plant, but its presence could be considered an indicator of human activity and invasive species dispersal (though dispersal may also be facilitated by animals, such as birds (Cao & Berent, 2019)). *S. dulcamara* was identified at four sites, two present and two absent; these sites were mainly in the southern half of Michigan, in Jackson, Lapeer, Newaygo, and Charlevoix counties (Table 2). Other than a marginally higher presence at 43°N latitude and below, this

species does not appear to be an indicator of any great disturbance in regards to *I. versicolor* presence/absence.

Nature of *I. versicolor* in disturbed sites

We have shown that sites with shorter distances to human disturbances tend to have a higher likelihood of co-occurrence with invasive species (especially *Typha*), but on the whole, *I. versicolor* sites were located at fairly short distances from human disturbances anyway. This could be an artifact of more *I. versicolor* populations being recorded where they are obvious, i.e. near roadsides or areas where humans frequently pass by. There are very few records included this study where sites were located several miles from any human disturbance. Indeed, more digitization efforts in herbaria have shown substantial collection biases (Daru et al., 2017).

Despite the aforementioned findings of *I. versicolor* competing poorly in disturbed sites, some observations support the claim that *I. versicolor* does well in disturbed sites. Site 06, located along Herron Rd. in Alpena County, was visited during both summers 2017 and 2018. The site was described as a mile-long stretch of unpaved road with deep ditches on either side, with *I. versicolor* appearing infrequently within said ditches. During summer 2017, the site appeared to have been completely cleared of woody vegetation on the eastern side (perhaps recently mowed for the installation of electrical poles), with an expanse of about ten meters from the road dominated by a prairie-like community. Beyond the cleared area and on the western side of the road was mesic forest. The original voucher, collected in 1972, stated that the specimen was collected in the eastern ditch; upon visitation in 2017, only 1-3 individuals were observed, all occurring singularly, at odd intervals on the eastern side of the road. About 12 individuals, occurring either singly or with two or three stems, were observed on the western, shaded side. We surmised that the recent clearing of the eastern side of the road and ditch had also severely cut down the *I. versicolor* population, and it was only now reestablishing, either from rhizomes or seeds coming from upstream of the ditch (though wild germination rates appear to be poor (Zhang et al., 2000)).

Upon visitation in 2018, when we checked the progress of the population, it appeared that the singular individuals we had observed the previous year had been quite successful. One individual, which had only one bloom and one leaf rosette in 2017, had 8 leaf rosettes in 2018 and multiple blooms producing seed. The high light intensity of the cleared eastern road as well as the opened habitat for *I. versicolor* to spread via rhizome likely led to high productivity for the eastern irises, and allowed them to continue reestablishing.

The high light requirements, and relatively slow spread, of *I. versicolor* (Coulber, 2019) may mean that periodic disturbance of *I. versicolor* habitat is actually beneficial to its persistence. If succession would be allowed unabated, large woody species with riparian habits such as *Alnus* spp. would be able to colonize and shade *I. versicolor*, leading to less bloom output and the potential for genetic stagnation due to no sexual reproduction occurring within the population (excessive shading leading to no bloom output was observed for sites 03, 21, 27, 56, and 72; Table 2). This, coupled with *I. versicolor*'s slow rhizomatous spread compared to other riparian species like grasses, sedges, or *Typha*, can lead to *I. versicolor* becoming outcompeted. With regular clearing of shading species, or species with less hardy or no rhizomes, *I. versicolor* can likely persist for long periods of time. The oldest voucher used in this study, collected 103 years before the 2017 visitation, may be an example of this exceptional persistence, in which *I. versicolor* was collected near a maintained boardwalk in Manistique on the shore of Lake Michigan.

### Soil texture and sedimentation rates

Soil textures for sites with present *I. versicolor* populations tended to have loamy soils, while sites with absent populations tended to have sandy soils or soils with excessive organic matter (Figure 10). Sandy or highly organic soils may have increased sedimentation, leading to covering and suffocating of *I. versicolor* rhizomes; suffocated rhizomes can be found under the substrate, decaying in the spring (Gates & Erickson, 1924).

Increased sedimentation and subsequent suffocation of *I. versicolor* rhizomes that may contribute to population absence would be expected to occur more frequently after deforestation, when soils are more susceptible to erosion (Daniels, 1987), or as a function of increased precipitation (Sweeney, 1992). Average annual precipitation has increased throughout Michigan over the past century (Figure 11), indicating that sedimentation rates may be a concern, especially as climate continues to change into the next century (Pryor et al., 2014). Examining voucher age and location in relation to deforestation events or other changes in land use would be an effective means of assessing how *I. versicolor* populations may respond to these disturbances as well.

### Study limitations

As mentioned previously, the unequal distribution of study sites throughout Michigan presents difficulty for drawing conclusions about *I. versicolor* presence/absence in relation to a latitudinal gradient. Unequal emphasis on identification of invasive species across sites also mitigates our ability to state conclusions about invasive co-occurrence with certainty (with the exception of *Typha* spp.). Determining that a site was the correct locality but that *I. versicolor* was not present was difficult to accomplish with certainty; it is possible that *I. versicolor* was present at some of the sites we called “absent”, but we simply were looking in the wrong place. Lastly, because of our emphasis on the impacts of human disturbances on *I. versicolor* populations, we did not examine the potential effects of “natural” disturbances, such as flooding, disease, or herbivory.

Future renditions of this study or similar projects would benefit from an equally enforced methodology across all sites, and an improved methodology for determining a population to be absent (perhaps searching for decaying rhizomes, as in Gates & Erickson, 1924). Introducing measures for monitoring water level at a site or the ability of the site’s soils to retain water, the microbial community and nutrient composition of soils, the reproductive phenology of *I. versicolor* across sites, and the interactions of *I. versicolor* with pollinators, herbivores, and pests would all be of use for disentangling the effects of these variables on *I. versicolor* and its habitat. In addition to these, the use of environmental niche modeling to predict the future distribution of *I. versicolor* and monitoring the areas within this predicted range would be interesting to further understand the niche requirements and dispersal ability of *I. versicolor*. Revisiting these sites periodically to more closely track the presence, disappearance, and even recolonization of *I. versicolor*, as well as changes in co-occurring taxa and the surrounding habitat, would provide valuable data for improving our understanding of what contributes to the ecology of *I. versicolor*.

Confirmation of our findings via experiments would also be useful. Specifically, greenhouse experiments of the competitive ability of *I. versicolor* against other species at different levels of pH, average temperature, and with disturbance regimes would aid in determining the causal factors of *I. versicolor* absence. Studies of the ability of *I. versicolor* to withstand sedimentation would also improve our understanding of this species. Finally, disentangling the apparent effects of disturbance, temperature, and invasion on *I. versicolor* will help in understanding conservation of this and similar species, as well as how compounding factors of human disturbance may contribute to changes in ecosystem composition and function.

### Aside: quality of herbarium data

The variance in the quality of location data obtained from herbarium specimens illuminates an issue within collections that must be addressed for future projects. A growing interest has been exhibited in mapping specimen localities for

public use (Daru et al., 2017), but this data is only as accurate as the data from which it was obtained. Particularly for older specimens, location data is at worst diminished to a nearby city or lake name, which may be useful for broad understanding of a species' habitable range but functionless for a project interested in examining the ecology of individual habitats. Fortunately, recent collectors have taken up the use of GPS coordinates or mapping software such as ArcGIS, GBIF, or iNaturalist to increase accuracy. Regulation of collection donations to include certain locality specifications – perhaps something as simple as mandating the inclusion of latitude/longitude data – would simplify the digitization process and facilitate returning to populations to monitor their health and longevity.

Furthermore, in the interest of monitoring population growth and decline, such information may be requested for collected specimens: photographs of the individual and the population, approximate measurements of the scope of a population (if applicable; measurements of population “length” and “width” may be difficult for a population that appears to stretch for several miles), and noticeable signs of disease, co-occurring species, or disturbances that may explain species colonization or extirpation. Additional metadata for herbarium specimens, especially in this era of “big data”, can only improve future research projects and our understanding of the world's flora.

### **Conclusions**

*Iris versicolor* is still present at most of the sites we examined, though populations may be shrinking or disappearing in relation to competition with species of *Typha*. *I. versicolor* populations may be most vulnerable in the southern margin of its range, where its habitat experiences higher rates of human disturbance, a greater dispersal of invasive species, and high average annual temperatures. However, there is also evidence that periodic human disturbance is beneficial to *I. versicolor*, perhaps in isolation of these other factors. Soils for present populations have consistent soil texture, but pH and electrical conductivity appear to be sensitive to other factors, particularly those that correlate with *Typha* co-occurrence. Visiting these sites periodically in coming years and adding more parameters to site assessments may uncover more interactions between *I. versicolor*, other native and invasive species, humans, and our environment.

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FABER ET AL. – HUMAN IMPACTS ON *IRIS VERSICOLOR* L.

(S1)	P/A	TA	C	ACA	R/CA	S/CA	pH	EC	Lat	D/DR	D/A	D/B	SD	IR	T	IP	SD	PA	LS	FR
P/A	1.00	0.37	0.45	0.19	0.37	0.33	-0.19	-0.22	0.36	-0.18	0.18	0.14	-0.24	-0.49	-0.40	0.19	-0.19	-0.42	-0.52	-0.42
TA	0.37	1.00	0.79	-0.01	0.06	-0.02	-0.31	-0.17	0.01	-0.19	0.09	-0.04	-0.01	-0.31	-0.14	-0.11	-0.17	-0.15	-0.19	-0.15
C	0.45	0.79	1.00	-0.10	0.06	0.09	-0.27	-0.22	0.16	-0.17	-0.02	0.01	-0.09	-0.38	-0.27	-0.01	-0.15	-0.19	-0.23	-0.19
ACA	0.19	-0.01	-0.10	1.00	-0.01	-0.03	-0.05	-0.10	0.27	-0.14	-0.10	0.04	-0.11	-0.03	0.11	0.03	-0.04	-0.08	-0.10	-0.08
R/CA	0.37	0.06	0.06	-0.01	1.00	0.88	0.19	-0.11	-0.07	0.01	0.16	-0.05	0.10	-0.21	0.10	-0.04	-0.15	-0.15	-0.19	-0.15
S/CA	0.33	-0.02	0.09	-0.03	0.88	1.00	0.29	-0.04	-0.08	-0.02	0.01	-0.02	0.05	-0.16	0.16	0.15	-0.13	-0.14	-0.17	-0.14
pH	-0.19	-0.31	-0.27	-0.05	0.19	0.29	1.00	0.35	-0.43	-0.17	-0.21	-0.11	0.00	0.29	0.55	-0.01	0.14	0.10	0.16	0.10
EC	-0.22	-0.17	-0.22	-0.10	-0.11	-0.04	0.35	1.00	0.02	0.09	-0.20	0.19	-0.01	0.05	0.33	0.00	0.01	-0.06	0.02	-0.06
Lat	0.36	0.01	0.16	0.27	-0.07	-0.08	-0.43	0.02	1.00	-0.10	-0.03	0.32	-0.38	-0.56	-0.40	0.05	-0.51	-0.50	-0.40	-0.50
D/DR	-0.18	-0.19	-0.17	-0.14	0.01	-0.02	-0.17	0.09	-0.10	1.00	0.01	-0.11	0.64	0.40	0.04	-0.15	0.07	0.53	0.38	0.53
D/A	0.18	0.09	-0.02	-0.10	0.16	0.01	-0.21	-0.20	-0.03	0.01	1.00	0.28	0.24	-0.13	-0.21	-0.07	0.10	0.00	-0.01	0.00
D/B	0.14	-0.04	0.01	0.04	-0.05	-0.02	-0.11	0.19	0.32	-0.11	0.28	1.00	-0.05	-0.10	0.03	-0.07	-0.06	-0.06	-0.05	-0.06
SD	-0.24	-0.01	-0.09	-0.11	0.10	0.05	0.00	-0.01	-0.38	0.64	0.24	-0.05	1.00	0.51	0.21	-0.14	0.28	0.75	0.57	0.75
IR	-0.49	-0.31	-0.38	-0.03	-0.21	-0.16	0.29	0.05	-0.56	0.40	-0.13	-0.10	0.51	1.00	0.29	0.10	0.50	0.78	0.84	0.78
T	-0.40	-0.14	-0.27	0.11	0.10	0.16	0.55	0.33	-0.40	0.04	-0.21	0.03	0.21	0.29	1.00	-0.35	0.32	0.22	0.28	0.22
IP	0.19	-0.11	-0.01	0.03	-0.04	0.15	-0.01	0.00	0.05	-0.15	-0.07	-0.07	-0.14	0.10	-0.35	1.00	-0.11	-0.08	-0.10	-0.08
SD	-0.19	-0.17	-0.15	-0.04	-0.15	-0.13	0.14	0.01	-0.51	0.07	0.10	-0.06	0.28	0.50	0.32	-0.11	1.00	0.30	0.53	0.30
PA	-0.42	-0.15	-0.19	-0.08	-0.15	-0.14	0.10	-0.06	-0.50	0.53	0.00	-0.06	0.75	0.78	0.22	-0.08	0.30	1.00	0.80	1.00
LS	-0.52	-0.19	-0.23	-0.10	-0.19	-0.17	0.16	0.02	-0.40	0.38	-0.01	-0.05	0.57	0.84	0.28	-0.10	0.53	0.80	1.00	0.80
FR	-0.42	-0.15	-0.19	-0.08	-0.15	-0.14	0.10	-0.06	-0.50	0.53	0.00	-0.06	0.75	0.78	0.22	-0.08	0.30	1.00	0.80	1.00

(S2)	P/A	TA	C	ACA	R/CA	S/CA	pH	EC	Lat	D/DR	D/A	D/B	SD	IR	T	IP	SD	PA	LS	FR
P/A	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TA	—	1.00	0.76	-0.09	-0.09	-0.15	-0.33	-0.16	-0.17	-0.16	0.02	-0.11	0.15	-0.29	0.01	-0.20	-0.15	—	—	—
C	—	0.76	1.00	-0.21	-0.13	-0.07	-0.27	-0.22	-0.01	-0.12	-0.12	-0.06	0.04	-0.36	-0.12	-0.11	-0.10	—	—	—
ACA	—	-0.09	-0.21	1.00	-0.09	-0.10	-0.02	-0.09	0.28	-0.13	-0.14	0.01	-0.11	0.14	0.23	0.00	0.00	—	—	—
R/CA	—	-0.09	-0.13	-0.09	1.00	0.86	0.36	-0.06	-0.30	0.11	0.10	-0.11	0.37	-0.07	0.31	-0.11	-0.11	—	—	—
S/CA	—	-0.15	-0.07	-0.10	0.86	1.00	0.48	0.05	-0.28	0.04	-0.05	-0.07	0.25	-0.01	0.35	0.10	-0.09	—	—	—
pH	—	-0.33	-0.27	-0.02	0.36	0.48	1.00	0.31	-0.39	-0.42	-0.15	-0.04	-0.17	0.22	0.44	0.04	0.09	—	—	—
EC	—	-0.16	-0.22	-0.09	-0.06	0.05	0.31	1.00	0.08	0.01	-0.16	0.44	0.21	0.03	0.31	0.07	-0.02	—	—	—
Lat	—	-0.17	-0.01	0.28	-0.30	-0.28	-0.39	0.08	1.00	0.26	-0.13	0.37	0.06	-0.32	-0.26	-0.03	-0.60	—	—	—
D/DR	—	-0.16	-0.12	-0.13	0.11	0.04	-0.42	0.01	0.26	1.00	0.02	-0.09	0.44	-0.02	-0.11	-0.15	-0.15	—	—	—
D/A	—	0.02	-0.12	-0.14	0.10	-0.05	-0.15	-0.16	-0.13	0.02	1.00	0.25	0.38	-0.23	-0.14	-0.10	0.09	—	—	—
D/B	—	-0.11	-0.06	0.01	-0.11	-0.07	-0.04	0.44	0.37	-0.09	0.25	1.00	-0.06	-0.06	0.15	-0.10	-0.09	—	—	—
SD	—	0.15	0.04	-0.11	0.37	0.25	-0.17	0.21	0.06	0.44	0.38	-0.06	1.00	-0.36	0.15	-0.17	-0.13	—	—	—
IR	—	-0.29	-0.36	0.14	-0.07	-0.01	0.22	0.03	-0.32	-0.02	-0.23	-0.06	-0.36	1.00	-0.01	0.41	0.17	—	—	—
T	—	0.01	-0.12	0.23	0.31	0.35	0.44	0.31	-0.26	-0.11	-0.14	0.15	0.15	-0.01	1.00	-0.33	0.33	—	—	—
IP	—	-0.20	-0.11	0.00	-0.11	0.10	0.04	0.07	-0.03	-0.15	-0.10	-0.10	-0.17	0.41	-0.33	1.00	-0.11	—	—	—
SD	—	-0.15	-0.10	0.00	-0.11	-0.09	0.09	-0.02	-0.60	-0.15	0.09	-0.09	-0.13	0.17	0.33	-0.11	1.00	—	—	—
PA	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
LS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
FR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Tables S1 and S2. Correlations between study parameters are given for all sites (S1) and only present and “extra” populations (S2). Colors scale to level of correlation. Darker green cells indicate high positive correlation between parameters, and darker red cells indicate high negative correlation between parameters. P/A = presence/absence, TA = total area, C = clumps, ACA = average clump area, R/CA = rosettes per clump area, S/CA = stems per clump area, pH = soil pH, EC = soil electrical conductivity, Lat = latitude, D/DR = distance from dirt road, D/A = distance from asphalt, D/B = distance from building, SD = shortest distance, IR = invasives richness, T = *Typha* species present, IP = *Iris pseudacorus*, SD = *Solanum dulcamara*, PA = *Phragmites australis*, LS = *Lythrum salicaria*, and FR = *Frangula* and *Rhamnus* species present. — values in S2 occur due to no variation in values for these metrics for present or “extra” populations (all values are either 0 or 1). Correlations discussed further in the text are shown in black boxes.