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Increasing Invasion of *Alliaria petiolata* (M. Bieb.) Cavara and Grande and Change in the Understory Community across Eight Years in a Fragmented Illinois Woodland

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Abstract

Alliaria petiolata (Bieb.) Cavara and Grande, a European biennial herb, has been a serious invader of natural areas and woodland communities of North America where it has been blamed for decreases in native species richness and community complexity. Most studies are conducted in places where strong impacts are already apparent. Studies analyzing the role of invasive species in pushing native species towards extinction or extirpation and documentation of invasion history are needed. This study was conducted at a previously grazed woodlot of second growth hardwoods. Herbaceous ground level plant species were surveyed in square meter plots for cover and species richness at different times across eight years and one year of plant biomass and cover data were collected. *Alliaria petiolata* increased in importance value (IV200) from 1.65 to 24.40 across the eight-year period. Excluding the 2002 sample set, plots with *A. petiolata* showed a significantly higher average richness than those without. Community composition changed significantly between all sample years. While there were no significant differences between native plant biomass within plots invaded by *A. petiolata* versus plots without *A. petiolata*, there was a significant difference between invaded and uninvaded plot total biomass. *A. petiolata* does not appear to be affecting species richness and native biomass only decreased when an *A. petiolata* biomass threshold was reached. This may indicate that species richness at sites may not be unduly affected by *A. petiolata* invasion or that species richness may not be a suitable variable to measure the effects of invasion. Future studies should concentrate on analyzing invasions using pre-invasion and post-invasion data to understand temporal effects of *A. petiolata* invasions on native species and other areas of potential long-term impact.

Keywords

Alliaria petiolata; Empty niche hypothesis; Plant invasions; Invasive species; Biomass; Garlic mustard; Novel weapons hypothesis; Temporal plant community changes

Introduction

Following habitat loss, invasive species are the second leading threat to biodiversity in the United States, imperiling 49% of threatened and endangered species [1]. Invasive species also offer the greatest threat to North American deciduous forest [2] where species composition of woodlands may change due to reduced species richness resulting from lower survival, fecundity, and regeneration of native species [3,4] or from altered competitive interactions [5].

The European biennial herb *Alliaria petiolata* ([Bieb.] Cavara and Grande) is a serious invader of natural areas and woodland communities of Illinois and elsewhere in North America [6-10]. It is able to establish in forest edges and within mature forest [6,7,11,12] affecting the fitness of understory plants and reducing native seed germination [13,14]. *Alliaria petiolata* is also a known producer of allelopathic chemicals, which are leached, exuded, or volatilized into the environment from the plant [15]. Allelopathy may suppress mycorrhizal fungi [16-20] and decrease survival of native plants [18,21] as it outcompetes extant vegetation for nutrients, water, or physical space [22].

Previous manipulation experiments involving field plots from which *A. petiolata* was, either herbicided or mechanically removed, failed to show a significant impact on species richness when compared with control plots, although evenness increased in some studies [12,13,23,24]. Similarly, removal of *A. petiolata* showed no alteration in the abundances of studied functional groups after two growing seasons [24]. The consequences of invasive species removal on the plant community, especially in places where strong impacts are already apparent, have received great research attention [4,12,13,23]. Few studies occurred in sites with pre-invasion or close to pre-invasion data in order to better document the role of invasive species in pushing native species towards extinction or extirpation [3]. The limited temporal duration of most studies does not allow a full understanding of the function of invasive species in plant communities [25] and long-term management observations are needed to see how invasive species removal affects plant composition [13]. Inferences on long-term impacts and population persistence based on short-term experiments could possibly be incorrect and unable to accurately predict the influence of these invasive species on plant communities [26].

Several hypotheses have been used to explain the success of invasive species in their novel range [27]. Among the potential mechanisms is the Novel Weapons Hypothesis. It suggests invasive plants secrete allelopathic chemicals that affect the fitness of neighboring plants in invaded sites, but are relatively ineffective against co-evolved neighbors in the species' native range [21]. As forest plant species are nearly 80% mycorrhizal, requiring a symbiotic association to facilitate nutrient uptake in nutrient-poor soils and help capture water when soil moisture is low [28,29], any hindrance of this relationship may be an effective mechanism for invasion. Of increasing interest to invasion ecology is the effect of invasive plants species on mycorrhizae in soil and how invasive plants can affect growth of nearby native plants [30].

Interactions among plants from different biogeographical areas suggest that the species composition of natural plant communities may be closely connected with species-specific interactions [21].

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Negative interactions between and within plant species are often seen when plants grow in close proximity as demands on resources are increased [31]. In the absence of competitors, individual plant species have shown increases in biomass and reproductive ability [32]. It is possible that species composition of woodlands may change as invasive species alter competitive interactions [5] for resources that may become limiting.

Using pre-*Alliaria petiolata* invasion baseline data from a small Illinois woodland fragment and comparing it to current herbaceous composition can eliminate problems associated with short-term or heavy impact removal studies. Results of increased levels of *A. petiolata* plant cover on native species cover and richness across time can be analyzed. If the introduction of *Alliaria petiolata* into Illinois forest fragments affects the herbaceous understory, then the comparison of current and historic data from Collins Woods is expected to show increased *Alliaria petiolata* invasion, lower species richness and an overall change in understory composition. Also, invaded plots are expected to have significantly less native biomass and cover compared to plots without *A. petiolata*. Should *A. petiolata* be able to invade plots without reducing native plant biomass or decreasing native species richness, its ability to acquire unused nutrients may be more strongly advanced as a mechanism explaining its invasiveness.

Methods

Collins Woods (Figure 1) is a previously grazed 5.36 ha woodland of second growth hardwoods owned and managed by the University of Illinois. Dominant tree genera in the western portion include *Quercus*, *Carya*, *Fraxinus*, and *Ulmus*. The eastern portion has a younger and denser mix of *Maclura pomifera* Schneid., *Gleditsia triacanthos* L., *Prunus serotina* Ehrh., *Quercus* spp., and *Carya* spp. A filled oxbow of the Salt Fork River cuts through the northwest corner of the woods. Collins Woods is bordered on the north and south by cultivated row crops, on the east by a roadway, and on the west by a housing development. A private residence constructed in 2005 lies on the south side of the easternmost portion of the site. Climatic conditions of the site are 41.3 inches of annual precipitation with 18.1 days annually above 90 degrees Fahrenheit and 122.1days annually below 32 degrees Fahrenheit.

Research was initiated in early summer (May to June) during 2002 with repeated observations in 2007 and 2010 repeating the same methodological procedures to follow the flora communities across time. For management purposes, the Collins Woods site has permanent steel T-posts placed throughout at 50-m intervals along cardinal directions. The 50-m intervals were further sub-divided at 10-meter intervals to generate a 10-m by 10-m grid pattern across the site. A 1-m^{2}quadrat was placed at each of the resulting grid intersections resulting in 449 plots. Plant species presence was recorded and plant cover was estimated to characterize the ground layer community (herbaceous species plus woody seedlings <2.0 cm dbh) at each plot. Ten plant cover classes, modified from Daubenmire [33], were utilized: (1) 0-5%, (2) 6-10%, (3) 11-15%, (4) 16-25%, (5) 26-35%, (6) 36-50%, (7) 51-65%, (8) 66-80%, (9) 81-95%, (10) 96-100%. Plant cover means were obtained by assigning the midpoint of the cover class to each observation. Individuals were identified to the species level according to Mohlenbrock [34,35] when possible, except for two large groups, grasses and sedges (recorded as graminoids), and the genera *Viola* and *Lonicera*. Unidentifiable species were either tagged *in situ* or collected for later identification.

Figure 1: Collins Woods. 40.08.15.98 N 88.02.09.90 W. Google Earth. March 28, 2005. February 12, 2012.

For the biomass survey, each intersection of the transects was assigned a number, excluding the oxbow region as recent rains had partially flooded this area, and a random number generator selected 101 intersections for the sampling of herbaceous species and seedlings (< 2.0 dbh and less than 1 meter tall) presence and aerial coverage within the ground layer community using 0.25-m^{2}quadrats. This specific plot size was used to better capture possible spatially dependent impacts as detrimental impacts were only experienced at a particular distance from *A. petiolata* individuals [19]. Species identification and plant cover means were determined as described above. For each 0.25-m^2 sample plot, the aboveground biomass was collected and separated into two groups: *Alliaria petiolata* biomass and native plant biomass to assess differences between groups. All plant biomass was dried at 60°C for 48 hours. The mean cover and biomass of native species, along with the mean cover and biomass of *A. petiolata*, were calculated.

Statistics

The Importance Value (IV200) of each species was determined as the sum of relative frequency and relative cover. Statistical analyses used R software version GUI 1.40-devel [36] and Primer6 for multidimensional scaling [37], which is a visualization tool to view sets of data. The points are arranged in three-dimensional space so that the distances between points indicate similarities among objects. Two points close together represent similar objects, and two points that are far apart represent two dissimilar objects. Species with IV200 ≥ 1.0 and present in both 2002 and 2010 were selected for multiple dimensional scaling (MDS), resulting in a capture of at least 75% of the total IV200 for each year. This method prevented rare species from being unduly influential in the model and should have eliminated any plant misidentification issues that may have occurred. Cover data were standardized and square root transformed before Bray Curtis similarity indexing was applied. Similarity measures were compared with years as a design factor using the Primer6 ANOSIM (analysis of similarity) procedure, which compares observed distributions with iteratively randomized permutations.

Data were analyzed using R software and the Classification and Regression Tree (CART) packages ctree (both use a $p<0.05$ to split) [38] and Welch's Two Sample T-test. Data were also analyzed by ctree, an R function used to understand variables for possible management decisions. Conditional inference trees, ctree, estimate a relationship by testing a null hypothesis of independence between any of the input variables and the response and stops if this hypothesis cannot be rejected. If the hypothesis is rejected, the input variable with strongest association to the response is selected. This association is measured by a p-value. A split in the data is then selected and the process repeats until there are no longer strong associations between the response and input variables [39].

Results

Tukey's Honest Significance Difference (HSD) test indicated a significant difference in total species richness between years at Collins Woods ($p<0.05$). Between sample years, both species richness in invaded plots and species richness in plots without *A. petiolata* increased between 2002 and 2007 and between 2002 and 2010 (Table 1). The importance (IV200) of *Alliaria petiolata* increased from 1.65 in 2002 to 16.48 in 2007 and then to 24.40 by 2010 (Table 2). Also, three of the four non-native species used in the Multidimensional Scaling (MDS) analysis increased its community importance across time, with *Rosa multiflora* being the only non-native species to decrease in importance (Table 2).Within years, significant differences were seen in years 2007 and 2010 between categories average species richness in plots with *A. petiolata* and average species richness in plots without *A. petiolata*. The IV200 for *Parthenocissus quinquefolia*, a native herbaceous species, had the greatest decline, from 40.8 to 12.8.

Significant differences were observed in herbaceous community data between 2002, 2007, and 2010 (Figure 2, $p<0.001$ for groups 2010-2007, 2010-2002, and 2002-2007 with $R=0.03$, 0.258, and 0.196 respectively) with increasing time difference between sampling periods with the 2002 and 2010 sampling interval having the largest R-value. Analysis of the 2002, 2007, and 2010 data after removal of the *A. petiolata* cover values continued to show a significant difference in community structure between plots, although the corresponding R-values were not as strong ($p<0.001$ for groups 2010-2007, 2010-2002, and 2002-2007 with $R=0.025$, 0.165, and 0.138 respectively).

Of the biomass plots sampled, only 22% did not contain *A. petiolata*. Plots with or without were significantly different in total biomass (Table 3) while presence of *A. petiolata* in the sampled plots did not significantly impact the biomass of co-occurring native species (Table 3). Native species richness was significantly greater in uninvaded plots (4.3 ± 1.4 species to 5.3 ± 1.6 species, $p<0.05$).

Table 1: Summary of herbaceous level survey for 2002, 2007, and 2010 in Collins Woods.

	2002	2007	2010
Average species per sample year	6.64 ± 2.48 (a)	6.98 ± 2.43 (b)	6.97 ± 2.20 (b)
Average species richness of plots with *A. petiolata*	6.39 ± 2.23 (a)	7.29 ± 2.20 (b)	7.33 ± 2.19 (b)
Average species richness of plots without *A. petiolata*	6.65 ± 2.49 (a)	6.51 ± 2.05 (b)	6.27 ± 2.08 (b)
Alliaria petiolata IV200	1.65	16.47	24.4
Percentage of plots containing *A. petiolata*	5%	60%	64%

All values significant at $p<0.05$

Note:

i. Lower case letters indicate comparisons by Tukey's HSD test between years.

ii. Significant differences were seen within years 2007 and 2010 between categories average species richness in plots with *A. petiolata* and average species richness in plots without *A. petiolata* using Welch's Two Sample test.

Table 2: Importance Values (IV200) of Collins Woods herbaceous understory species for three sampling years 2002, 2007, and 2010 (IV200 numbers were determined as the sum of relative frequency and relative cover).

Species		**Year**	
	2002	**2007**	**2010**
Sanicula gregaria	25.06	31.81	26.72
Alliaria petiolata*	1.65	16.48	24.44
Parthenocissus quinquefolia	40.80	19.55	12.80
Toxicodendron radicans	12.37	13.32	11.84
Cryptotaenia canadensis	7.37	8.54	11.33
Pilea pumila	0.25	8.41	11.03
Viola spp.	12.57	11.43	8.13
Impatiens pallid	2.86	2.48	7.43
Geum canadense	10.76	10.56	7.11
Graminoids	11.14	9.51	6.94
Ribes missouriense	6.05	6.86	6.38
Circaea lutetiana	2.58	4.45	5.12
Ambrosia trifida	1.20	2.18	4.57
Smilax hispida	4.62	3.53	4.06
Loniceraspp. *	0.04	3.64	3.96
Rosa multiflora*	6.76	2.34	3.86
Celtis occidentalis	4.23	6.15	3.82
Osmorhiza claytonii	0.90	0.79	3.06
Lysimachia nummularia*	0.001	3.05	2.74
Gleditsia triacanthos	2.21	2.37	2.30
Geumvernum	4.13	0.00	1.79

* Indicates a non-native species

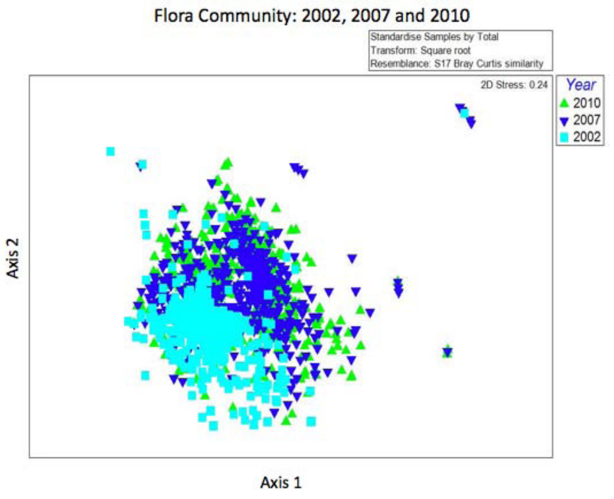

Figure 2: Multidimensional scaling of sampling years 2002, 2007, and 2010. Pairwise test using ANOSIM indicate significant differences $p<0.001$ for groups 2010-2007, 2010-2002, and 2002-2007 with $R = 0.03$, 0.258, and 0.196 respectively.

Increased *A. petiolata* biomass reduced native species richness (Figure 3) and increasing *A. petiolata* biomass reduced native species biomass (Figure 4). Without *A. petiolata,* increased native species cover was associated with increased native species richness (Figure 4).

Discussion

The community of Collins Woods has shifted since the initial sampling in 2002 and *A. petiolata* has subsequently become a significant species. By removing *A. petiolata* from the data and performing multidimensional scaling on the combined 2002, 2007, and 2010 plant community data, significant community differences were still observed, indicating that community differences were not simply due to a larger *A. petiolata* population. Unfortunately, this information can only indicate there are differences seen in the plant community and cannot describe to what extent *A. petiolata* caused or was associated with the shift or if there were other ecological pressures.

The dissimilar IV200 for *A. petiolata* between 2007 and 2010, while still having close to the same percentage, 60% and 64%, of occupied plots could be an artifact of the biennial lifecycle of *A. petiolata*. As IV200 is a composite of cover and frequency, the difference in cover over time, rather than a difference in frequency caused the difference in IV. If *A. petiolata* plants observed in 2002 resulted from a single founding population, then 2007 would be a rosette year and 2010 an adult year with more overall relative coverage due to the larger cover associated with the bolting stage of adult *A. petiolata* plants.

Table 3: Plot survey data. Letters indicate Welch's Two Sample T test was performed between categories.

	Average Biomass (g)	std
Total Biomass, Invaded Plots	22.1 (a*)	±8.86
Total Biomass, Un-invaded Plots	18.0 (a*, b)	±7.98
Native Biomass, Invaded Plots	16.0 (b)	±7.64

*indicates a significant difference of p=<0.05; All other comparisons were nonsignificant (p-values>0.05, b=0.33)

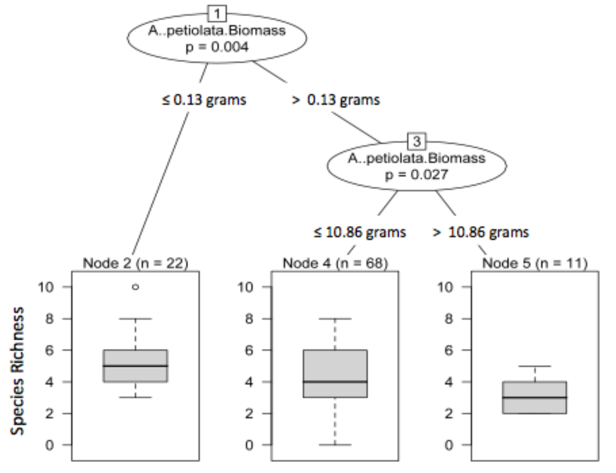

Figure 3: Species richness in response to *A. petiolata* biomass.

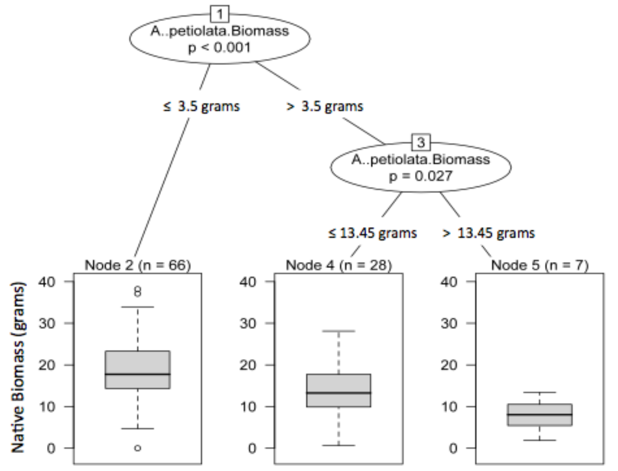

Figure 4: Native species biomass in response to *A. petiolata* biomass.

The 2002 sample is the only data set where average species richness in plots without *A. petiolata* is larger than the plots with *A. petiolata*. This may be due to the effects of *A. petiolata* having a stronger impact in its initial infestation compared to an impacted site that has adapted to its presence [40].The inconsistent results shown here for species richness may indicate and support the idea species richness is an insensitive response variable for invasion studies [24,41].

Forest understory communities are dynamic systems and temporal changes are expected, but invasion by *A. petiolata* and other non-natives may be shifting the community to an alternative dynamic state. Past use of the site, prior to the 2002 sampling period, may have already changed the community type to select for grazing increasers such as *Sanicula gregaria, Cryptotaenia canadensis* and *Ribes missouriense,* but selection pressure may now come from introduced species. The potential of plant invasions to elicit differential impacts on specific species [24,42] may explain single species observations. Depending on the robustness and requirements of a species, there may be differential impacts by *A. petiolata* and this is an area where research is needed.

It is important to reiterate the past history of this site and other study sites as invasion by *A. petiolata* may also have larger impacts on undisturbed versus disturbed forest [42] and thus produce results seen here at Collins Woods, a previously grazed site. This may explain why species richness did not decrease, even with the increasing abundance of *A. petiolata*. In the short-term, many invasions have resulted in increased species richness at local levels [43] before impacts on native species occur. Conversely, a study analyzing changes across fifty years found similar insignificant differences between invaded and uninvaded stands of three invasive plants, including *A. petiolata* [41].

In the biomass study, *A. petiolata* appears to be replacing one native species in invaded plots at this particular grain of 0.25-m^2. *Alliaria petiolata* has been shown to inhibit beneficial mutualistic fungi most readily at a 10-cm distance [19] and to form very dense stands [6], therefore the mechanism here for lower species richness in 0.25-m^2 invaded plots might be spatially impacted. The density dependence of *A. petiolata* and its spatially different life cycling may allow some native species to survive depending on neighborhood influence [44] as soil communities and native species cover have been able to recover with reduced *A. petiolata* cover [45], but further research involving null models is needed to verify distance as a mechanism and to rule out sampling artifacts resulting from plot size [46].

The observed decrease of native species biomass with increased *A. petiolata* was expected, but the insignificant difference of native biomass between plots with and without *A. petiolata* was not. If *A. petiolata* was present in previous years, degradation of the soil microbial community may have already occurred, leading to an impact even though individuals of *A. petiolata* were currently absent [40]. This implies the presence or absence may not be a sensitive variable in sites with invasion history. Studies have shown even with removal of *A. petiolata,* declines in the levels of arbuscular mycorrhizal fungi colonization due to past presence of *A. petiolata* may reduce growth rates of native mycorrhizal species and the rate at which they can reoccupy vacated space [45]. Where *A. petiolata* was present and its biomass was high, the biomass of native species was lower than was typically present in plots without *A. petiolata*, suggesting a threshold of greater than 3.5 g of *A. petiolata* biomass is necessary to impact native species biomass. This may indicate impacts are dependent on the continuous presence of large amounts of biomass and that *A. petiolata*'s biennial lifecycle may allow for a commensurate rebound of native plants. This may explain why invaded versus uninvaded native biomass was insignificantly different. Conversely, there may be an alternative to the Novel Weapons Hypothesis, the Empty Niche Hypothesis.

The Empty Niche Hypothesis suggests invasive species can use or have access to resources in the novel range that native species do not utilize [47]. This would suggest there should be no measurable amounts of difference between invaded and uninvaded plots for native species and a significant increase for total biomass of invaded plots, results both seen in this study. This hypothesis also predicts the insignificant differences seen in species richness for the invaded and uninvaded plots in other studies, although sampling scale may be important [46]. It would be difficult to consider the Empty Niche hypothesis as the most important invasion hypothesis when considering *A. petiolata*'s impacts on arbuscular mycorrhizal fungi communities and subsequent decreases in survival of native plants [42] and its effects on mycorrhizal inoculum potential [48], but a combination of these two hypotheses may explain *A. petiolata*'s competitive ability. There is a possibility that resource and non-resource mechanisms, such as allelopathy, work simultaneously, but vary depending on particular species [49].

Studies analyzing forest communities and individual plant species across time scales greater than seen in this study may allow researchers a better understanding of the possible significant or insignificant in situ impacts of *A. petiolata*. Future research is needed to substantiate the Empty Niche Hypothesis as a mechanism of invasion for *A. petiolata*. This may be especially important, as many recent studies have implicated *A. petiolata*'s allelopathic characteristics as its mechanism for invasion. This study indicates the Empty Niche Hypothesis may help explain the invasion strategy of *A. petiolata* along with the Novel Weapons Hypothesis, but further research analyzing resource acquisition and competition between *A. petiolata* and native plants is needed to answer which hypothesis better explains *A. petiolata* invasion or to what extent these two hypothesis work together.

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