Response of the invasive Alliaria petiolata to extreme temperatures and drought

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Abstract. Alliaria petiolata, a strict biennial in North America, can have an annual alternating high abundance of rosettes and flowering plants. We monitored changes in abundance of rosettes and flowering plants in permanent plots (2004–2014). Three times during our study, the alternating yearly cycle was not observed (2007–2008, 2008–2009, and 2013–2014). We concluded stochastic extreme climate events (ECEs), deviating from long-term climatic data norms (10th or 90th percentile), likely caused negative organism responses. Long-term data from a local NOAA station located 25 km from our study site included monthly data (1) total precipitation, (2) number of days with >0.13 cm precipitation, and (3) mean and minimum temperatures. September 2007 met the criteria for ECEs for all monthly variables. We first observed A. petiolata on our study site in 1988, and by the early 1990s, it was abundant. To determine whether September 2007 significantly differed from other September (1984–2014), we used six variables related to drought: (1) total precipitation, (2) number of days with precipitation, (3) number of contiguous days without precipitation, (4) mean monthly temperature, (5) mean maximum daily temperature, and (6) the number of days with temperatures >30°C. The first two variables likely increase plant stress as they decrease, whereas stress declines as the remaining variables decrease. We used the six variables to generate a principal component analysis (PCA) biplot. Axes 1 and 2 accounted for 74.3% of the variance. Record-breaking minimum temperatures (ECEs) for January (2009) and February–March (2014) likely reduced rosette abundance and disrupted reestablishment of alternating high abundance of rosettes and flowering plants. Our data suggest that a single ECE variable, minimum temperature, and multiple ECE variables related to drought likely had negative effects on A. petiolata.

Key words: declining alternating abundance; extreme climate; flowering plants; negative response; rosettes; stochastic weather events.

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INTRODUCTION

Invasive species can enter locations where changes in climate may have negative or positive effects on their distribution and abundance. Extreme climate events (ECEs) may enhance invasions by reducing native competitors and increasing habitats suitable for invasion (Diez et al. 2012). Some invasive species may be
initially well adapted to climatic conditions in their invaded areas; however, climate change can result in some invasive species declining in abundance and shifting their distribution range (Merow et al. 2017). Experimentally, research indicates invasive species have adapted to their novel environment compared with native range populations of conspecifics (Flory et al. 2011). In this manuscript, we consider the response of the invasive plant *Alliaria petiolata* to ECEs over a period of eleven years in long-term research plots.

The native Eurasian species, *Alliaria petiolata*, first introduction in North America was likely on Long Island, New York, USA, in 1868, and is now a widely distributed ground-layer species in eastern deciduous forests of North America (Nuzzo 1991, Rodgers et al. 2008). Multiple introductions of the species, and the lack of inbreeding depression (Durka et al. 2005, Mullarkey et al. 2013), resulted in *A. petiolata* colonization of 38 states, including Alaska, in the United States, and five Canadian provinces (EDDMMaps 2018).

*Alliaria petiolata* is a strict biennial in North America. Following cold moist stratification, seeds germinate in February and March, and the biennial spends its first year as basal rosettes. In the second year, rosettes persist until they bolt in March and transition to mature plants that flower between mid-March and May. Mature fruits (siliques) develop from late May into June. Peak seed rain occurs in August and September (Anderson et al. 1996, Herold et al. 2011, Loebach and Anderson 2018). *A. petiolata* has high seed output compared with other woodland species with annual seed rain of 9500 to more than 100,000 seeds per m² (Anderson et al. 1996, Rodgers et al. 2008, Pardini et al. 2009). In addition, *A. petiolata* has a competitive advantage over some native species, for space, nutrients, and light (before the tree canopy is well-developed), and with early seed germination and bolting of rosettes (Myers and Anderson 2003, Engelhardt and Anderson 2011).

In eastern deciduous forests, *A. petiolata* is most abundant in the northeastern and midwestern portions of the United States (Welk et al. 2002). Nevertheless, several studies found or predicted a declining abundance and/or shifting range of *A. petiolata* on a regional scale in these areas (Lankau et al. 2009, Lankau 2011, Merow et al. 2017). There are two primary explanations for the decline of *A. petiolata*. In eastern deciduous forests, 70–90% of native plants form mycorrhizal associations, which increase plant uptake of specific inorganic nutrients and water. Loss of the association reduces growth and reproductive success of mycorrhizal-dependent plants (Roberts and Anderson 2001, Stinson et al. 2006, Callaway et al. 2008, Wolfe et al. 2008, Li et al. 2019). When *A. petiolata* initially invades a site, it has a high level of the allelochemical sinigrin, which is toxic to some other plants and mycorrhizal fungi, resulting in increased interspecific competitive ability. However, over time *A. petiolata* abundance increases and native species decline, resulting in a reduction in interspecific competition. Reduced competition then favors selection for a decrease in the energetically costly defensive chemicals, further resulting in a decline. A reduction in the production of allelochemicals favors intraspecific competition but lessens the competitiveness of *A. petiolata* against native species, causing a decline in the abundance of the invasive species (Lankau et al. 2009, Cantor et al. 2011, Lankau 2011, Evans et al. 2016). In addition, there is a decline in species richness of soil microbial communities as the period of invasion increases, followed by greater resistance to *A. petiolata*’s effects. Over time, *A. petiolata* alters soil microorganism composition and abundance in a way that is unfavorable to itself (Lankau 2011). Other research indicates that decline or increase in the species abundance relates to the length of time that it occurs in an area (Lankau et al. 2009, Evans et al. 2016). A second explanation for population declines of *A. petiolata* is applicable to ECEs and climate variables causing drought. In this manuscript, we report on the potential effect of ECEs and drought on the abundance of *A. petiolata*, which has not been previously examined.

Several sources documented the annual alternating abundance of rosettes and mature plants (Baskin and Baskin 1992, McCarthy 1997, Winterer et al. 2005, Bauer et al. 2010, Van Riper et al. 2010, Davis et al. 2014). Usually, a year with a low abundance of rosettes and a high abundance of adult flowering plants is followed by a year with low abundance of adults, but a high abundance of rosettes. Because of the small number of rosettes in the first year, due in part to

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competition from mature plants, few rosettes transition to mature flowering plants in the following year. However, heavy seed production by mature plants can result in high rosette abundance in the second year, that is, the year following high mature plant abundance (Winterer et al. 2005, Pardini et al. 2009, Bauer et al. 2010, Davis et al. 2014). Pardini et al. (2009) modeled the stage-specific demography of *A. petiolata* using three difference equations for the abundance of seeds, rosettes, and adults. The model supported the dynamics of alternating abundance of rosettes and mature plants. They suggested that this dynamic is generated by deterministic rules and is more likely to occur in dense core populations than in isolated low-density satellite populations, which is congruent with the results reported by Davis et al. (2012). However, Pardini et al. (2009) also reported that stochastic events, such as droughts, could interrupt the population cycling, such as occurred during an extreme drought in the fall of 2007 at their study site (Tyson Research Center, Eureka, Missouri, USA), which eliminated most first-year rosettes. Reducing the abundance of rosettes in 2007 resulted in few mature plants in the following year and two consecutive years of high abundance of rosettes, presumably resulting largely from seeds present in the seed bank in 2008. They suggested that the population would quickly return to two-stage cycles following this weather event (Pardini et al. 2009).

**Methods**

Our study site has four blocks each containing 60 2.5 × 2.5 m treatment plots equally divided among a control and two removal treatments of *A. petiolata*, early removal of rosettes in March before they bolt and previous year’s seed production germinates, and late (May) removal of flowering plants (see Bauer et al. 2010 for details). Each treatment and control plot has a 50 × 50 cm sampling quadrat located in the center of the plot. We estimated cover of rosettes and cover and counts of mature flowering plants in the 50 × 50 cm quadrats. Rosettes were counted in two-decimeter (10 × 10 cm) quadrats, one each placed in the northeast and southeast corners of the sample plot. These data were collected from 2004 to 2019. However, we are presenting only data from the 80 control sampling plots for this study and only for the years 2004–2014. We analyzed count data to determine years that did not have high abundance of mature plants following a year of high abundance of rosettes. We tested for significant differences in density between years for rosettes and mature flowering plants separately. Rosette plants were counted in mid-summer 2007 (19, 24, and 25 July) in the 50 × 50 cm quadrats to determine the proportion of rosettes that transitioned to mature plants in spring 2008 (19–20 April and 17–19 May).

**Analysis of the count data for rosettes and mature flowering plants**

We analyzed count data for rosettes and mature plants separately in May of each year to determine which years were significantly different for each cohort using SAS (2013). Data were ln-transformed using PROC GLIMMIX with a log-link function to meet the assumptions of a Poisson distribution with the fixed effect being year. PROC GLIMMIX is a SAS program that allows general linear mixed modeling of data that may include internal correlations and/or represent a nonnormal distribution (Schabenberger 2005). We used LSmean tests with a Tukey-Kramer adjustment for multiple comparisons to test for differences among the counts of rosettes (decimeter quadrats) and mature plants (50 × 50 cm quadrats) separately to determine significant differences among years for samples taken in 2004–2014. However, the long-term monitoring of *A. petiolata* continues (Fig. 1).

To determine the proportion of rosettes that transitioned to mature plants, the same analysis was used to test for significant differences between the number of rosettes counted in mid-summer (July) of 2007 compared with the counts of mature flowering plants sampled in April and May 2008 using 50 × 50 cm quadrats. We present back-transformed LSmeans and standard errors for each sample (Fig. 2).

**Transition of rosettes to mature flowering plants**

We modified the procedure of Pardini et al. (2009), to examine survivorship of 2007 mid-summer rosettes to mature flowering plants in May 2008. The 2007 quadrats were arranged in groups with similar numbers of rosettes and
were ordered by increasing mean numbers of rosettes in the groups. For the groups, the proportion of rosettes surviving to maturity was regressed against the ln density of rosettes of the previous year (Fig. 3). The regression coefficient was used as \( s_3 \), the probability of summer rosettes survival from July to maturity in early May, by Pardini et al. (2009). The coefficient becomes increasingly negative as the portion of summer rosettes transitioning to mature plants decreases as a function of high density of summer rosettes and consequently higher levels of intraspecific competition and ECEs in our study.

**High rosette density did not result in high density of mature plants**

The years 2009 and 2014 had low densities of mature plants in the 50 × 50 cm quadrats following a year of high densities of rosettes in 2008.
percentile, generally de-  
centile, or above the 90th, 95th, or 99th  
De-  
and 2013 based on counts in the 10 \times 10 \text{ cm}  
quad-rats, respectively. However, we did not have  
counts of rosettes in mid-late summer in 2008  
and 2013 using 50 \times 50 \text{ cm} quadrats. Neverthe-  
less, the low abundance of mature plants follow-  
ing a year of high density of rosettes strongly  
suggests that ECEs (cold temperatures) may  
have been a major factor in reducing abundance  
of mature plants.

**Defining extreme climate events**

Various sources defined ECEs as events deviat-  
ing from climatic data norms. NOAA (National  
Oceanic and Atmospheric Administration 2018)  
characterized ECEs as occurring in the outer 10%  
of climatic data norms (10th or 90th percentile).  
The Intergovernmental Panel on Climate Change  
(IPCC; Seneviratne et al. 2012) reported that in  
scientific literature typical indices “…include the  
amount, percentage, or fraction of days with  
maximum temperature ($T_{\text{max}}$) or minimum  
temperature ($T_{\text{min}}$), below the 1st, 5th, or 10th  
percentile, or above the 90th, 95th, or 99th  
percentile, generally defined for given time  
frames (days, month, season, annually)…”  
(Seneviratne et al. 2012, Ummenhofer and Meehl  
2017). For example, ECEs were defined as the  
extreme 1% of annual values (Diez et al. 2012),  
5% of annual values (Smith 2011a), or 10%  
(Knapp et al. 2015). Other sources have defined  
ECEs as events deviating two to three standard  
deviations from climate data norms (Palmer and  
Raisanen 2002, Luceño et al. 2006, Rahmstorf and  
Coumou 2011). However, Smith (2011a) noted that  
many ecological studies focus on the effect of  
climate extremes on ecological systems without  
providing a definition of ECEs based on  
statistical criteria and long-term data. Addition-  
ally, there should be an ecological response to  
ECEs (Smith 2011b), and according to Bertin  
(2008), phenology is a sensitive monitor of  
climate.

We used NOAA climate data from Chenoa,  
Illinois, located 25 km northeast of our study  
site, to determine the occurrence of ECEs for  
temperature and precipitation. Collection of data  
for precipitation and temperature began in 1944  
and 1951, respectively (NOWData NOAA, online  
weather data. Weather station at Chenoa, Illinois,  
USA, 1944–2014. https://w2.weather.gov/climate/  
xmacis.php?wfo=ilx).

When climate data for specific dates were  
unavailable, we substituted data from another  
NOAA station located in Normal, Illinois, USA,  
which is 23 km southwest of our field study site.  
The variables we had were number of days with  
$>0.13$ cm of precipitation, mean monthly temper-  
ature, and total precipitation for September and  
in minimum temperatures for January 2009, and  
February and March 2014.

We used Pearson’s correlations to compare  
climate data between the two NOAA stations. We  
compared minimum temperatures for the three  
months (January, February, and March):  
$R_{190} = 0.9493$, $P < 0.001$, number days with  
precipitation $>0.13$ cm ($R_{69} = 0.8528$, $P < 0.001$),  
mean monthly temperature ($R_{56} = 0.8315$,  
$P < 0.001$), total monthly precipitation  
($R_{68} = 0.8936$, $P < 0.001$), and all four variables  
combined ($R_{383} = 0.9931$, $P < 0.001$). The number  
of days the weather station had missing data for  
in minimum temperatures, days with precipitation  
$>0.13$ cm, mean monthly temperature, total  
monthly precipitation, and all variables  
combined, respectively, were 0, 3, 5, 2, and 10.

We considered ECEs to be events based on  
rank, occurring in the 90th or 10th percentile,  
and having a significant ($P < 0.05$) departure  
from the mean of the long-term data using t-  
tests. All data sets were tested for normality  
using the Shapiro-Wilk test, and data were trans-  
formed when necessary. To determine whether  
September 2007 climate variables were qualified  
as ECEs, we used data taken between 1944 and  
2014 for total precipitation, number of days with  
precipitation $>0.13$ cm (Knapp et al. 2015), and  
mean monthly temperature (1951–2014)  
(Table 1). To meet the assumptions of normality,  
total precipitation data were transformed using  
$\ln(x + 1)$.

**Factors contributing to drought after A. petiolata  
invasion**

*Alliaria petiolata* was first reported on our study  
site in 1988, on property owned by the Park-  
Lands Foundation, a nonprofit organization, and  
was well established by the early 1990s. How-  
ever, *A. petiolata* was present in nearby areas,  
including Ewing Park in Bloomington, Illinois,  
USA, 25 km away from our study site, in the  
early 1980s. To provide a comprehensive exami-  
nation of stochastic factors that may have
induced moisture stress, and potentially rosette mortality, during the time that the invasive species was on our study site, we used daily data for September 1984–2014. For each of these 31 yr, we obtained information for six factors influencing moisture stress. The six variables are (1) total precipitation, (2) number of days with precipitation, (3) number of contiguous days without precipitation, (4) mean monthly temperature, (5) mean maximum daily temperature, and (6) the number of days with temperatures >30°C. NOAA records maximum and minimum temperatures daily, and these two temperatures are recorded as the mean daily temperature.

NOAA defines “total precipitation for the day to the nearest hundredth of an inch. This total can include all forms of precipitation, both liquid and water equivalent of any snow or ice that occurred (T = Trace, some precipitation fell but not enough to measure)” (https://w2.weather.gov/climate/f6.php). At the Chenoa, Illinois, NOAA Station, precipitation, and maximum and minimum temperature were measured at 6:00 PM.

Droughts are extreme weather events that occur at a specific location and time of year, and normally can be as uncommon as the 10th or 90th percentile estimated from observations (IPCC 2014). Variables 4, 5, and 6 were included because increases in temperature can enhance transpiration rates and increase loss of soil moisture (Andregg et al. 2013, Vincente-Serrono et al. 2014, Urban et al. 2017). We tallied these variables manually using the NOAA Chenoa, Illinois, data. We did not determine whether all the variables included ECEs, because our focus was on years with A. petiolata present on our study site and adjacent areas. To test for significant differences between September 2007 data and the means of each of the six variables, we calculated means and standard deviations separately for the six variables across all years excluding 2007 (Table 2). For each variable, we used t-tests to determine whether there were statistically significant differences (P < 0.05) between separate means of variables, and the corresponding value of the variables for 2007. We tested for normality using the Shapiro-Wilk procedure. To meet the normality criterion, total precipitation and number of days with temperatures >30°C were In and square-root-transformed, respectively.

To obtain a comprehensive effect of the six variables on increasing plant stress, we ranked the 31 yr from highest to lowest stress for each of the six variables. For two of the variables, total precipitation, and number of days with precipitation, plant stress decreased as the level of the variable increased. For the four remaining variables, plant stress increased as the values of these four variables increased. Separately, for the six variables, we ranked each of the 31 yr from 1 (highest) to 31 (lowest), based on the relative degree of drought stress that plants would experience. If the rank scores for two or more years tied for a single variable, we averaged the rank scores. For example, if three years tied for the same rank score (5, 5, and 5) collectively they would occupy the ranks 5, 6, and 7. All three years were assigned the mean of the occupied ranks, which is 6.

We summed rank scores across six variables for each year (1984–2014). Summed rank scores potentially ranged from 6 to 186. To test for significant differences among years, we removed the year being tested from the data, and the summed rank scores for the remaining 30 yr were tested for normality separately. We used a t-test to determine whether the summed ranks scores for 2007 were significantly different from the mean of the other 30 yr combined (Table 3).
We also used principal component analysis (Peck 2010) to determine how the six factors, described above, differed among years (1984–2014) and the importance of individual variables in determining differences among years. We extracted six axes, and biplots were obtained using the three axes (Axes 1 and 2 and Axes 1 and 3) that accounted for the greatest amount of variation in the data set. Eigenvectors, eigenvalues, and Pearson’s correlation coefficients were obtained between ordination axes and each of the six response variables (Table 4).

Table 2. We examined six weather variables in September (1984–2014) that can negatively affect plants.

| Year or statistic | Total PPT (cm) | ln total PPT | No. days w/PPT | Contig. No. days w/no PPT | Mean monthly temp. °C | Mean max. daily temp. °C | Days with temp. >30°C | SQRT (days + 2) > 30°C |
|------------------|---------------|-------------|----------------|--------------------------|----------------------|------------------------|----------------------|------------------------|
| A                |               |             |                |                          |                      |                        |                      |                        |
| 1984             | 5.6           | 1.72        | 14             | 6                        | 17.8                 | 24.4                   | 9                    | 3.32                   |
| 1985             | 3.9           | 1.36        | 6              | 12                       | 18.9                 | 25.3                   | 10                   | 3.46                   |
| 1986             | 14.5          | 2.67        | 13             | 6                        | 20.4                 | 26.7                   | 8                    | 3.16                   |
| 1987             | 4.2           | 1.44        | 5              | 11                       | 18.9                 | 25.7                   | 2                    | 2.00                   |
| 1988             | 7.3           | 1.98        | 6              | 10                       | 19.6                 | 27.8                   | 7                    | 3.00                   |
| 1989             | 9.7           | 2.28        | 10             | 7                        | 16.4                 | 23.1                   | 0                    | 1.41                   |
| 1990             | 2.5           | 0.93        | 6              | 6                        | 19.6                 | 26.1                   | 6                    | 2.83                   |
| 1991             | 8.2           | 2.11        | 8              | 5                        | 19.2                 | 25.3                   | 11                   | 3.61                   |
| 1992             | 11.4          | 2.43        | 10             | 4                        | 17.8                 | 24.1                   | 2                    | 0.00                   |
| 1993             | 16.0          | 2.77        | 9              | 9                        | 16.2                 | 21.4                   | 0                    | 1.41                   |
| 1994             | 7.2           | 1.97        | 7              | 16                       | 19.3                 | 25.4                   | 8                    | 3.16                   |
| 1995             | 4.8           | 1.57        | 4              | 11                       | 17.2                 | 24.2                   | 2                    | 0.00                   |
| 1996             | 9.1           | 2.21        | 6              | 11                       | 17.8                 | 24.3                   | 1                    | 1.73                   |
| 1997             | 3.6           | 1.28        | 9              | 7                        | 18.7                 | 25.1                   | 2                    | 0.00                   |
| 1998             | 1.0           | 0.1         | 5              | 13                       | 21.8                 | 28.3                   | 9                    | 3.32                   |
| 1999             | 3.4           | 1.22        | 5              | 13                       | 17.9                 | 25.7                   | 8                    | 3.16                   |
| 2000             | 8.8           | 2.17        | 6              | 9                        | 19.7                 | 27.3                   | 11                   | 3.61                   |
| 2001             | 8.1           | 2.09        | 8              | 7                        | 17.7                 | 24.2                   | 3                    | 2.24                   |
| 2002             | 4.1           | 1.41        | 5              | 14                       | 20.2                 | 27.4                   | 9                    | 3.32                   |
| 2003             | 5.8           | 1.76        | 8              | 8                        | 17.7                 | 25.0                   | 2                    | 0.00                   |
| 2004             | 3.8           | 1.34        | 1              | 15                       | 19.6                 | 26.9                   | 7                    | 3.00                   |
| 2005             | 5.8           | 1.76        | 7              | 15                       | 21.8                 | 29.1                   | 16                   | 4.24                   |
| 2006             | 10.0          | 2.3         | 9              | 7                        | 17.6                 | 23.3                   | 0                    | 1.41                   |
| 2008             | 22.9          | 3.13        | 12             | 12                       | 19.3                 | 25.5                   | 6                    | 2.83                   |
| 2009             | 3.5           | 1.25        | 7              | 14                       | 18.5                 | 24.3                   | 0                    | 1.41                   |
| 2010             | 8.9           | 2.19        | 11             | 7                        | 19.3                 | 26.8                   | 8                    | 3.16                   |
| 2011             | 10.1          | 2.31        | 11             | 4                        | 16.9                 | 22.8                   | 4                    | 2.45                   |
| 2012             | 12.1          | 2.49        | 5              | 9                        | 18.2                 | 25.2                   | 5                    | 2.65                   |
| 2013             | 5.0           | 1.61        | 6              | 8                        | 20.4                 | 27.8                   | 8                    | 3.16                   |
| 2014             | 12.0          | 2.48        | 5              | 15                       | 17.8                 | 24.3                   | 2                    | 2.00                   |
| B                |               |             |                |                          |                      |                        |                      |                        |
| Mean             | 7.77          | 1.88        | 7.47           | 9.63                     | 18.74                | 25.4                   | 5.53                 | 2.64                   |
| SD               | 4.6           | 0.63        | 2.89           | 3.57                     | 1.38                 | 1.70                   | 4.10                 | 0.7807                 |
| SE               | 0.846         | –0.17       | 0.529          | 0.653                    | 0.259                | 0.32                   | 0.749                | 0.143                  |
| df               | 29            | 29          | 29             | 29                       | 29                   | 29                     | 29                   | 29                     |
| t-value          | 7.77          | 14.82       | 10.30          | 14.75                    | –9.33                | 70.16                  | –11.31               | –9.58                  |
| Pr > t           | < 0.0001      | < 0.0001    | < 0.0001       | < 0.0001                 | < 0.0001             | < 0.0001               | < 0.0001             | < 0.0001               |
| Shapiro-Wilk     | 0.0113        | 0.5667      | 0.2422         | 0.4277                   | 0.4422               | 0.9831                 | 0.49                 | 0.0576                 |

Notes: The results of statistical testing indicate that September 2007 is significantly different from other September from 1984 to 2014 combined. The P-value is presented for the Shapiro-Wilk test for normality.
Extreme climate events for January 2009, and February and March 2014

During our study, there were two years, other than 2007, when a year with a high abundance of rosettes was not followed by a high abundance of flowering plants in the next year. These times were 2008 and 2013 when rosettes transitioning to mature plants were fewer than anticipated for 2009 and 2014, respectively (Fig. 1). An examination of Chenoa weather data for 2008, 2009, 2013, and 2014 indicated that the low density of mature flowering plants in 2009 and 2014 was likely due

Table 3. Scores are ranked by years for the six variables and summed from lowest to highest for each year.

| Year | Total PPT | No. days W/PPT | Max no. cont. days w/no PPT | No. days with temp. >30°C | Mean monthly temp °C | Mean max daily temp °C | Sum ranks |
|------|-----------|----------------|-----------------------------|--------------------------|----------------------|------------------------|----------|
| 1984 | 13        | 31             | 28                          | 6                        | 22                   | 21                     | 121      |
| 1985 | 8         | 10             | 11                          | 5                        | 16                   | 17                     | 67       |
| 1986 | 29        | 30             | 27                          | 9                        | 4                    | 10                     | 109      |
| 1987 | 10        | 4              | 14                          | 21                       | 15                   | 13                     | 77       |
| 1988 | 17        | 11             | 15                          | 14                       | 10                   | 5                      | 72       |
| 1989 | 23        | 25             | 25                          | 28                       | 30                   | 29                     | 160      |
| 1990 | 3         | 12             | 26                          | 16                       | 8                    | 11                     | 76       |
| 1991 | 19        | 19             | 29                          | 3                        | 14                   | 16                     | 100      |
| 1992 | 26        | 26             | 31                          | 22                       | 21                   | 27                     | 153      |
| 1993 | 30        | 22             | 18                          | 29                       | 31                   | 31                     | 161      |
| 1994 | 16        | 16             | 2                           | 10                       | 11                   | 15                     | 70       |
| 1995 | 11        | 3              | 13                          | 23                       | 28                   | 25                     | 103      |
| 1996 | 22        | 13             | 12                          | 27                       | 23                   | 24                     | 121      |
| 1997 | 6         | 23             | 24                          | 24                       | 17                   | 19                     | 113      |
| 1998 | 1         | 5              | 9                           | 7                        | 1                    | 3                      | 26       |
| 1999 | 4         | 6              | 8                           | 11                       | 20                   | 12                     | 61       |
| 2000 | 20        | 14             | 17                          | 4                        | 7                    | 7                      | 69       |
| 2001 | 18        | 20             | 23                          | 20                       | 25                   | 26                     | 132      |
| 2002 | 9         | 7              | 6                           | 8                        | 6                    | 6                      | 42       |
| 2003 | 14        | 21             | 22                          | 25                       | 26                   | 20                     | 128      |
| 2004 | 7         | 1              | 4                           | 15                       | 9                    | 8                      | 44       |
| 2005 | 15        | 17             | 3                           | 1                        | 2                    | 1                      | 39       |
| 2006 | 24        | 24             | 21                          | 30                       | 27                   | 28                     | 154      |
| 2007 | 2         | 2              | 1                           | 2                        | 3                    | 2                      | 12       |
| 2008 | 31        | 29             | 10                          | 17                       | 12                   | 14                     | 113      |
| 2009 | 5         | 18             | 7                           | 31                       | 18                   | 23                     | 102      |
| 2010 | 21        | 27             | 20                          | 12                       | 13                   | 9                      | 102      |
| 2011 | 25        | 28             | 30                          | 19                       | 29                   | 30                     | 161      |
| 2012 | 28        | 8              | 16                          | 18                       | 19                   | 18                     | 107      |
| 2013 | 12        | 15             | 19                          | 13                       | 5                    | 4                      | 68       |
| 2014 | 27        | 9              | 5                           | 26                       | 24                   | 22                     | 113      |

Notes: The first two variables, total precipitation and number of days with precipitation, increase plant stress as they decrease, whereas the remaining variables increase stress as they increase. Scores range from 1 (most stress) to 31 (least stress).

Table 4. Pearson’s correlations and significance between PCA axes and six potential moisture stress variables.

| Variables                           | Axis 1     | Axis 2     | Axis 3     | Axis 4     | Axis 5     | Axis 6     |
|-------------------------------------|------------|------------|------------|------------|------------|------------|
| Total PPT                           | 0.56***    | -0.49*     | -0.63***   | 0.014      | 0.14       | 0.08       |
| No. days w/PPT                      | 0.62***    | -0.65***   | 0.11       | 0.26       | -0.28      | -0.07      |
| No. contiguous days with no PPT     | -0.67***   | 0.44*      | -0.51**    | 0.16       | -0.20      | -0.10      |
| Mean monthly temp. °C               | -0.88***   | -0.34      | 0.02       | 0.02       | -0.12      | 0.28       |
| Mean max. daily temp. °C            | -0.61***   | -0.61***   | -0.05      | -0.45*     | -0.03      | -0.15      |
| No. days with temp. >30°C           | -0.77***   | -0.39      | 0.08       | 0.42*      | 0.23       | -0.10      |

Note: *P < 0.05; **P < 0.01; ***P < 0.001.

Extreme climate events for January 2009, and February and March 2014

During our study, there were two years, other than 2007, when a year with a high abundance of rosettes was not followed by a high abundance of flowering plants in the next year. These times were 2008 and 2013 when rosettes transitioning to mature plants were fewer than anticipated for 2009 and 2014, respectively (Fig. 1). An examination of Chenoa weather data for 2008, 2009, 2013, and 2014 indicated that the low density of mature flowering plants in 2009 and 2014 was likely due
to the below normal temperatures that occurred in January 2009, and February and March 2014. It is possible some rosettes were severely damaged or eliminated during a single day with extremely cold temperatures. Using NOAA data (1951–2014), we found that January 2009 (−31.7°C), and February (−30°C) and March 2014 (−21.1°C) each had a record minimum temperature for one day; however, March 2002 had the same minimum temperature as March 2014. Unfortunately, we did not initiate our sampling of rosettes and mature plants until 2004.

We tested the three-monthly minimum temperatures for ECEs separately using rank, percentiles, and t-tests to determine significant differences between the other years (1951–2014) and January 2009, and February and March 2014. For the t-tests, data were tested for normality using the Shapiro-Wilk procedure. Data for March were transformed [ln (value/−21.1)] to normalize the data (Table 6).

RESULTS

Variation in rosettes and mature plants density and transition of rosettes (2007) to mature plants

For stem count data, the GLIMMIX convergence criterion was satisfied (PCONV = 1.11022−8). The fixed effect (time) was significant for rosettes ($F_{10, 276} = 156.33, P < 0.0001$) and mature flowering plants ($F_{10, 276} = 276.67, P < 0.0001$) for the 2004–2014 data analysis. Fig. 1 shows the back-transformed least-squares means separately for rosettes and mature flowering plants that were sampled in 10 × 10 cm and 50 × 50 cm quadrats for the two cohorts, respectively. Means with lower case letters are for rosette plants and uppercase letters are for mature flowering plants. Within an age cohort (rosettes or mature flowering plants), means with the same letters are not significantly different.

During the first four years of our study, rosettes and mature plants showed alternating years of high abundance (Fig. 1). Mature plants had high abundance in 2004 and 2006 and rosettes in 2005 and 2007 (Bauer et al. 2010). However, beginning in 2008 there was a disruption of the alternating year cycle of abundance of the two cohorts, and rosettes had high abundance and mature flowering plants had low abundance. This unexpected change in abundance of rosettes and mature plants occurred because there was a reduction in the proportion of rosettes in 2007 transitioning to mature plants in 2008, even though in 2008 rosettes in control plots reached their second highest density during our study (2004–2014). The high abundance of rosettes was likely due in part to reduced competition from mature plants and a high seed abundance in the seed bank.

Transition of July 2007 rosettes to April and May 2008 mature plants

The GLIMMIX convergence criterion (PCONV = 1.11022−8) was satisfied. The fixed effect (time) was significant ($F_{2, 232} = 232.15, P < 0.0001$). Back-transformed least-squares means ±SE for rosettes in July 2007 and mature flowering plants in April and May counted in the 50 × 50 cm quadrats were

- 6.14 ± 0.072 ($t = 26.94, P < 0.0001$),
- 0.34 ± 0.11 ($t = 2.68, P > t < 0.0082$),
- 0.46 ± 0.108 ($t = 3.51, P > t < 0.0001$),

for the three samples, July, April, and May, respectively (Fig. 2). Least-squares mean estimates for the 2007 July sample were significantly different from 2008 samples taken in April ($t = 16.56, df = 154, P > t < 0.0001$) and May ($t = 16.30, df = 154, P > t < 0.001$), and April and May samples were not significantly different from each other ($t = −0.64, df = 154, P > t < 0.7983$). The percentage of rosettes sampled in July 2007 transitioning into flowering plants in April and May 2008 was 5.5% and 7.5%, respectively.

Using the procedure of Pardini et al. (2009), we examined the survivorship of 2007 mid-summer rosettes to mature flowering plants in May 2008. The proportion of rosettes surviving to maturity was regressed against the ln density of rosettes of the previous year. Of the 78 quadrats (50 × 50 cm), six did not have rosettes in 2007. We used the regression coefficient ($s_3$) as the probability of summer rosettes survival from July to maturity in early May, following Pardini et al. (2009). The coefficient becomes increasingly negative as the portion of summer rosettes transitioning to mature plants decreases. For our data (2007 rosettes to 2008 mature plants), the coefficient ($s_3$) of Pardini et al. (2009) was −0.4645 (Fig. 3).

Using long-term data from Chenoa, Illinois, USA, we tested for the occurrence of ECEs in September 2007 (https://w2.weather.gov/climate/
The available data were total precipitation \((\ln(x + 1) – \text{transformed})\), number of days with >0.13 cm of precipitation, and mean temperature (Table 2). For September 2007, total precipitation, number of days with >0.13 cm of precipitation, and mean monthly temperature ranked 4/71, 6/71, and 60/64, respectively, and occurred in the 6th, 8th, and 94th percentiles, respectively. The \(t\)-tests for all three variables were significant at \(P < 0.000, P = 0.0455, \) and \(P < 0.0001, \) respectively (Table 2).

Comparing drought factors of September 2007 to September 1984–2006 and 2008–2014 combined

Based on \(t\)-tests, the year 2007 had significant differences for all six variables from the 30 other years combined (Table 2). However, the year 2007 had the highest stress ranking (first) among the 31 yr for maximum number of contiguous days without precipitation and ranked second for four other stress factors: total PPT, number of days with precipitation, maximum number of contiguous days without precipitation, number of days with temperature \(>30^\circ C\), and mean maximum daily temperature. The year 2007 also ranked third for mean monthly temperature (Table 3). By comparison, September 2005 had two moisture stress factor values that ranked slightly higher than September 2007, number of days with temperatures \(>30^\circ C\), and mean monthly temperature. However, September 2005 received 4.8 times as much precipitation as 2007, and the maximum number of contiguous days without precipitation was 7 days fewer for 2005 than 2007. In 2004, September had only one day with precipitation, whereas this month had a cooler mean monthly temperature, fewer contiguous days without precipitation, only one day with temperature \(>30^\circ C\), and received three times as much total precipitation as September 2007 (3.8 vs. 1.2 cm). The year 1998 received less precipitation than 2007 (1.1 vs. 1.2 cm).

Principal component analysis

Six PCA axes were extracted, as many as there were variables. Pearson’s correlations between the six variables and axes are given in Table 4. We are using only Axes 1, 2, and 3 to determine stress among the 31 yr. All six variables were significantly correlated \((P < 0.05)\) with Axis 1. The two variables that reduced moisture stress (total precipitation and number of days with precipitation) had positive correlations with Axis 1, whereas the four remaining variables that increase moisture stress were negatively correlated with Axis 1. Three variables were significantly negatively correlated with Axis 2, total precipitation, days with precipitation, and mean maximum daily temperature, and one was positively correlated, number of contiguous days with no precipitation. Axis 3 has two significant negative variables, total precipitation and number of contiguous days with no precipitation. Axes 1, 2, and 3 accounted for 48.9%, 25.4%, and 11.6%, of the variance, respectively, and collectively accounted for 86.0% of the total variance (Table 5).

We prepared PCA ordination biplots of the years (1984–2014) on the first three axes (Fig. 4). On the biplots, years were plotted on the first three PCA axes and eigenvectors for each response variable were multiplied by 3.45 to occupy the same space as sample unit (years) space (Peck 2010). The trajectories of the number of days with precipitation and total precipitation were away from 2007, and toward years 2008, 2010, and 2011.

The six variables are (1) total precipitation, (2) number of days with precipitation, (3) number of contiguous days without precipitation, (4) mean monthly temperature, (5) mean maximum daily temperature, and (6) the number of days with temperatures \(>30^\circ C\) (Table 6). The trajectory of each variable is shown in the PCA biplot. Capital letters A through F designate the six variables in the biplot: for the upper panel (A), Axes 1 and 2,

| Axis | Eigenvalues | Variance (%) | Cumulative variance (%) |
|------|-------------|--------------|------------------------|
| 1    | 2.934       | 48.896       | 48.896                 |
| 2    | 1.527       | 25.447       | 74.343                 |
| 3    | 0.697       | 11.620       | 85.966                 |
| 4    | 0.485       | 8.030        | 94.049                 |
| 5    | 0.220       | 3.666        | 97.715                 |
| 6    | 0.137       | 2.285        | 100.00                 |

Table 5. The percentage of variance explained by a given axis is the ratio of the axis eigenvalue to the total sum of all eigenvalues.
In general, in Fig. 4, the trajectory of the variables away from 2007 is 1, 2, and 4 and variables toward 2007 are 3, 5, and 6. Other than 2007 (rank 12, Table 3), the highest ranking years for stress are 1998 (26), 2005 (39), 2002 (42), and 2004 (44), and the lowest ranking years for stress are 1993 (161), 2011 (161), 1989 (160), and 2006 (154).

**Table 6.** We tested for extreme climate events (ECEs) for January 2009, and February and March 2014 using minimum temperatures.

| Statistic        | 2009 January | 2014 February | 2014 March |
|------------------|--------------|---------------|------------|
| N                | 63           | 63            | 63         |
| Rank             | 1st          | 1st           | 1.5        |
| Percentile       | 1.5%         | 1.5%          | 2.3%       |
| Mean             | –22.0        | –19.0         | –11.7      |
| SD               | 4.8          | 4.9           | 3.8        |
| t-test           | –65.31       | –79.22        | –68.31     |
| P-value          | <0.001       | <0.001        | <0.001     |
| Min. temp. °C    | –31.7        | –30.0         | –21.1      |
| Shapiro-Wilk     | 0.9699       | 0.9802        | 0.9645     |
| P-value          | 0.1260       | 0.4056        | 0.0665     |

*Notes:* We used rank, percentiles, and t-tests to determine significant differences between all other years (1951 and 2014) and January 2009, and February and March 2014. All data were negative, and –21.1 °C was the coldest minimum March temperature for all years, except 2002 that had the same minimum temperature. Tests for normality used the Shapiro-Wilk test. P-Values < 0.05 reject normality.

**Effect of extreme cold temperature**

Minimum temperature rank for January 2009 (–31.7°C) and February 2014 (–30.0°C) was first (1st), and the rank was 1.5 for March 2014 (–21.1°C), because March 2002 had the same minimum temperature. The percentile was 1.5% for January and February and 2.35% for March. All three months had significant t-tests and normal distributions (Table 6).

**DISCUSSION**

Several authors noted that invasive and native organisms can be good indicators of ECEs (Sparks et al. 2000, Bertin 2008, Hellmann et al. 2008, Smith 2011a, b, Cleland et al. 2012, Knapp et al. 2015). In our study, we examined extreme climate events as factors likely causing disruption of the annual alternating abundance of rosettes and mature flowering plants and reducing the abundance of *A. petiolata*. Pardini et al. (2009) did not use data from the droughty autumn 2007 in their study, but they reported that the coefficient ($s_3$), for 2003 rosettes transitioning to mature plants in May 2004, was –0.2890. In contrast, our study showed there was a large difference in $s_3$ between the study of Pardini et al. (2009) and our study, –0.2890 and –0.4645, respectively. Our data indicate high levels of moisture stress and intraspecific competition among rosettes could have caused greater mortality among July rosettes on our study site (2007–2008) than August rosettes on the site studied by Pardini et al. (2009) in 2003–2004. Thus, a stochastic event (i.e., drought in September 2007) likely reduced the number of rosettes transitioning to mature plants in April and May.

Fig. 4. We used a principal component analysis ordination and biplot using six variables related to moisture and temperature stress to determine whether a decline in *A. petiolata* in 2007 was due to unsuitable weather conditions.

(A) 4, (B) 1, (C) 2, (D) 6, (E) 3, and (F) 5; for the lower panel (B), Axes 1 and 3, (A) 4, (B) 1, (C) 2, (D) 5, (E) 3, and (F) 6. 

Effect of extreme cold temperature

Minimum temperature rank for January 2009 (–31.7°C) and February 2014 (–30.0°C) was first (1st), and the rank was 1.5 for March 2014 (–21.1°C), because March 2002 had the same minimum temperature. The percentile was 1.5% for January and February and 2.35% for March.
in 2008. This demographic change resulted in low abundance of mature plants in 2008, which should have been a year of high abundance for mature plants and a year of low abundance of rosettes. Nevertheless, the high abundance of rosettes in 2008 presumably resulted from reduced competition from mature plants, which are strong competitors of rosettes (Pardini et al. 2009, Herold et al. 2011), and germination of seeds in the seed bank. Pardini et al. (2009) suggested A. petiolata would return to the alternating abundance of rosettes and flowering plants in two years after 2007. Our data indicate that while there was a high abundance of rosettes and a low abundance of mature plants in 2008, it was not followed in 2009 by high abundance of mature plants and a low abundance of rosettes.

The extreme cold temperature of January 2009 appeared to be the cause of the low number of 2008 rosettes transitioning to mature plants in 2009. After 2010, our data suggested the two-stage cycle was becoming reestablished with an increased number of rosettes in 2011 and 2013 and mature flowering plants in 2012. However, extremely cold temperatures in February and March 2014 may have been the cause of a reduced proportion of rosettes (2013) becoming mature plants in 2014. Reduction of 2008 and 2013 rosettes in 2009 and 2014 likely prevented reestablishment of the alternating abundance of rosettes and mature A. petiolata plants on our study plots.

The rankings of each of the six climatic variables showed that overall the drought year (2007) had the most extreme September drought conditions of the years 1984–2014. Of these six variables, 2007 had the highest ranking for the number of continuous days without precipitation. This result is consistent with the report by Knapp et al. (2015), indicating extreme dry years are distinguished by the number of dry days between rain events. In the PCA ordination, the number of continuous days without precipitation, number of days with precipitation, and total precipitation were strong factors separating dry years from wet years. The number of days with temperatures >30°C and mean temperature for the month were somewhat less important in separating dry years from wet years. However, when mean temperature for September 2007 was tested for significant difference across all years for which we have data (1951–2014), September 2007 met our criteria for ECEs (ranked fifth of 64 yr, 94th percentile) and had a significant \( P = 0.0495 \) t-test score, as previously noted. The years 1998 and 2005 tied for the warmest years (during 1951–2014) and met our standard for ECEs. Nevertheless, the warm mean temperature of 2007, which met our criteria for an ECE, likely reduced available soil moisture through evaporation and enhanced plant transpiration (Sturm et al. 1998, Vicente-Serrano et al. 2014, Urban et al. 2017) and contributed to increased moisture stress on A. petiolata plants. The year 2007 ranked second for lowest total precipitation and 1998 ranked first. In addition, both years qualified as ECEs based on precipitation data (1944–2014) and occurred in the 4th (1998) and 6th (2007) percentile. Thus, the negative effects of drought (below-average precipitation) on plants can be enhanced by few days with precipitation and normal temperature.

Several studies found that A. petiolata grows better in wetter habitats or years than in drier ones. Byers and Quinn (1998) reported that rosette mortality was higher in upland than in floodplain forests in dry summer months. Meehins and McCarthy (2001) concluded that survival of rosettes to reproduction was significantly greater for plants in lowland \((0.44 \pm 0.05)\) than upland forests \((0.17 \pm 0.07)\) and suggested that soil moisture played a dominant role in the success of plants in lowland forests. Englehardt and Anderson (2011) compared A. petiolata biomass in a dry spring (2005) when March, April, and May received 47%, 66%, and 17% of normal precipitation, respectively, and in a wet spring (2006) that had 179%, 198%, and 64% of normal precipitation for the three months, respectively. There was no significant difference in A. petiolata total biomass between the two years, but root mass was significantly greater in the dry spring (2005), and significantly greater fruit mass occurred in the wet spring (2006). Plants allocate greater amounts of resources (root mass) to enhance water uptake in drier years than wet years, and smaller allocation of resources to fruit production (Grace 1997, Quezada and Gianoli 2010).

We concluded the extreme cold temperature of January 2009 may have been the cause of the small number of rosettes transitioning to mature plants in 2009. After 2010, our data indicated the two-stage cycle was reestablishing with an
increasing number of rosettes in 2011 and 2013 and adults in 2012. However, extremely cold temperatures in February and March 2014 likely caused a reduced proportion of rosettes (2013) becoming mature plants in 2014. This reduction in rosettes may have prevented reestablishment of the alternating abundance of rosettes and mature *A. petiolata* on our study plots. Thus, it is likely that the extremely cold conditions of February and March 2014 reduced the number of rosettes that transitioned to adult *A. petiolata* plants. Consequently, at three times (2007, 2009, and 2014) during our study, extreme stochastic climate events likely interrupted the alternating abundance of rosettes and mature flowering plants. While several other causes were proposed for the decline of *A. petiolata*, it seems that none of them could cause a rapid decline of *A. petiolata* such as ECEs may be capable of doing. Nevertheless, our findings do not conflict with other studies related to the decline of *A. petiolata*.

It appears that changing climatic conditions can alter the status of invasive species by improving climate conditions that favor invasive species, and make the climate less suitable for native species, which are unable to adjust to the changing climate, and/or expand the range of the invasive species that tend to be adapted to a wider range of climatic conditions than native species (Dukes and Mooney 1999, Bertin 2008, Capdevila and Zilletti 2008, McEwan et al. 2009, Walther et al. 2009). Nevertheless, several studies reported that climatic conditions in novel environments and levels of climate change could influence the spread and success of invasive species differently (Diez et al. 2012). Merow et al. (2017) concluded in New England warming temperatures might reduce the abundance of *A. petiolata*, but not eliminate it in the southern portion of its range in New England and expand its current geographic distribution in northeastern United States and adjacent Canada due to climate change. For example, Corbin et al. (2017) reported that in their study area (Adirondack Park, New York, USA) the number of known populations of *A. petiolata* tripled from 2006 to 2015. Thus, it appears that while *A. petiolata* is expanding its current geographic distribution in northeastern United States and adjacent Canada due to climate change, in the southern portion of the invasive species distribution in the midwestern and northeastern United States, populations of the invasive species have declined (Merow et al. 2017).

However, invasive species populations may evolve adaptations in response to changing climates, allowing them to persist in their invaded habitats and improve their competitiveness over native species in locally adapted populations (Blossey and Notzold 1995, Dukes and Mooney 1999, Hellmann et al. 2008, Flory et al. 2011, Blossey et al. 2017). The capacity of an invasive plant *Microstegium vimineum* (stiltgrass) to evolve adaptive changes in a novel environment was documented by Flory et al. (2011). These results support the hypothesis that invasive species may undergo evolutionary changes in response to novel climatic conditions.

Research has demonstrated that local adaptation may be occurring in North American populations of *A. petiolata*, based on common garden seed germination (Blossey et al. 2017). Germination was highest for seeds collected from northern locations (IL, MN, and Ontario), which had a climate overlap with the common garden, whereas southern locations (DC, GA, and KS) had a lower climate overlap. However, stochastic events, such as ECEs, may affect evolutionary changes for *A. petiolata* and other species. Nevertheless, more stable climate changes, such as consistent warming climates, may drive evolutionary changes and range expansion (Merow et al. 2017). *A. petiolata* seed banks can retain viable seeds for as long as 13 yr (Blossey et al. 2017), and a population that has declined in size can recover rather quickly if there is a reasonable time between stochastic ECEs, as is suggested by our data.

**Conclusions**

Our research appears to have shown that climate events including drought and extreme cold can interrupt the alternating dominance of the two-stage life cycle by increasing mortality of a susceptible life stage, that is, rosettes of *A. petiolata*. This event may have the potential to affect evolution of locally adapted populations as well as the abundance and spread of invasive species.

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**DATA AVAILABILITY**

Data are available from the Illinois State University Archive, ISU ReD: https://doi.org/10.30707/fpbiosci/NIVS7941