


LETTER

Residence time determines invasiveness and performance of garlic mustard (*Alliaria petiolata*) in North America

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Abstract

While biological invasions have the potential for large negative impacts on local communities and ecological interactions, increasing evidence suggests that species once considered major problems can decline over time. Declines often appear driven by natural enemies, diseases or evolutionary adaptations that selectively reduce populations of naturalised species and their impacts. Using permanent long-term monitoring locations, we document declines of *Alliaria petiolata* (garlic mustard) in eastern North America with distinct local and regional dynamics as a function of patch residence time. Projected site-specific population growth rates initially indicated expanding populations, but projected population growth rates significantly decreased over time and at the majority of sites fell below 1, indicating declining populations. Negative soil feedback provides a potential mechanism for the reported disappearance of ecological dominance of *A. petiolata* in eastern North America.

Keywords

Alliaria petiolata, Brassicaceae, long-term monitoring, negative soil feedback, plant invasions, population growth rate, residence time.

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INTRODUCTION

Biological invasions can reshape local economies and ecological interactions, mutualistic relationships and ecosystem processes such as decomposition, carbon sequestration and energy flow (Keller *et al.*, 2007; Bradley *et al.*, 2010; Clavel *et al.*, 2011; Hof *et al.*, 2011; Powell *et al.*, 2011; Wardle *et al.*, 2011; Hooper *et al.*, 2012; Boyd *et al.*, 2013; Simberloff *et al.*, 2013; Caplan *et al.*, 2015). However, the vast majority of naturalised species are benign with little recognisable impacts. Predicting and distinguishing potential invasive threats for species that have not yet arrived, or just have become established, has occupied scientists and policy makers for decades (Williamson and Fitter, 1996; Lonsdale, 1999; Smith *et al.*, 1999; Sakai *et al.*, 2001; Keller *et al.*, 2007; Hayes and Barry, 2008; Elliott-Graves, 2016; Hulme and Bernard-Verdier, 2018; Divšek *et al.*, 2019; Fourniera *et al.*, 2019; Muthukrishnan *et al.*, 2019). Understanding each species' demography is at the core of separating major invasive plants that show rapid local population increase, establishment of local dominance or range expansions (Gurevitch *et al.*, 2011) from those that become established but remain minor members of local plant communities.

A phenomenon that has received increased attention is whether introduced species go through boom and bust cycles,

ultimately becoming non-threatening members of local communities. Specifically, whether species that pass from naturalisation, to establishment, to ecological dominance with major impacts, can subsequently decline in dominance. Simberloff and Gibbons (2004) mentioned 17 examples of species exhibiting such patterns, most without documented mechanisms for declines, but cautioned that future potential population declines of invaders should not be a reason to postpone control and management since irreversible impacts may occur. Since this publication, declines have been reported for introduced marine (Benkwitt *et al.*, 2017) and freshwater fishes (Gibson-Reinemer *et al.*, 2017), a marine crab (Forsstrom *et al.*, 2018), noctuid moths (Elkinton *et al.*, 2006), yellow crazy ants in Australia (Cooling and Hoffmann, 2015), Argentine ants in New Zealand (Cooling *et al.*, 2012), other ant species (Lester and Gruber, 2016; Tartally *et al.*, 2016), the invasive grasses *Microstegium vimineum* in North America (Flory *et al.*, 2011; Stricker *et al.*, 2016), and *Spartina alterniflora* in China (Tang *et al.*, 2012), grey squirrels in Ireland (Sheehy and Lawton, 2014), a land snail (Orstan and Cameron, 2015) and birds (Aagaard and Lockwood, 2016; Aagaard *et al.*, 2016). A review of plant invasions in North America (Warren *et al.*, 2019) and New Zealand (Diez *et al.*, 2010) suggests that most species follow a pattern of establishment, increase and spread followed by declines after 100–300 years of local residence.

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Mechanisms driving these declines are often unclear, but most appear associated with accumulation of natural enemies (herbivores, parasites, diseases) as a function of residence time and this is well documented for introduced plants (Andow and Imura, 1994; Mitchell and Powers, 2003; Carpenter and Cappuccino, 2005; Diez *et al.*, 2010).

Here we report on work considering local and regional population dynamics of *Alliaria petiolata* (garlic mustard), a European biennial herb in temperate North America. Range expansion and local abundance increases of *A. petiolata* in the 20th century co-occurred with native forest understory plant declines. In response, land managers deployed a range of control treatments, but only achieved temporary suppression, prompting research into biological control (Blossey *et al.*, 2001; Davis *et al.*, 2006; Gerber *et al.*, 2007). We established a regional long-term monitoring program at 16 sites to establish baseline population dynamics (measuring recruitment as number of rosettes in the first year, survival of rosette cohort to adult plants and fecundity as number of siliques/stem) to enable future assessments in response to a possible introductions of specialised herbivores (Blossey *et al.*, 2001). Particularly rosette survival and seed output are crucial parameters in the demography of *A. petiolata* (Davis *et al.*, 2006), thus our data cover the most important factors in the life cycle of this biennial plant. Based on experience conveyed to us by land managers we predicted sustained local annual *A. petiolata* populations and vigour (number of stems, height, cover and reproduction) with some annual fluctuations in recruitment driven by local differences in climate but no sustained declines. Several years into this monitoring program, we observed local *A. petiolata* declines that lacked an obvious cause (such as presence of above ground natural enemies). We used an exploratory assessment of potential underlying mechanisms at a location where the chronosequence of *A. petiolata* arrival, spread and decline was well established to test for potential negative soil feedback (van der Putten *et al.*, 2013). We show that (1) widespread *A. petiolata* declines are a function of local residence time; (2) regional differences in patterns of decline may reflect invasion histories and (3) projected population growth rates decline to < 1 (indicating shrinking populations) after 10–20 years. Our exploratory assessment leads to a new hypothesis that changes in population growth rates are a response to negative soil feedback, but this hypothesis needs confirmation at additional sites and across the range of *A. petiolata* in North America.

METHODS

Experimental organism

Alliaria petiolata (Brassicaceae) is an obligate biennial first recorded in North America in 1868 on Long Island, New York (Nuzzo, 1993). Seeds germinate in spring, and rosettes form in early summer. Rosettes overwinter, grow rapidly the following spring and bolt. Seeds ripen and drop in early summer forming a seedbank that remains viable > 10 years (Blossey *et al.*, 2017). Phenology of *A. petiolata* varies with local climates, and after 150 years of residence time in North America, rapid evolutionary changes and phenotypic plasticity

resulted in locally adapted populations with striking differences in germination requirements and secondary chemistry (Lankau *et al.*, 2009; Lankau, 2012b; Evans *et al.*, 2016; Blossey *et al.*, 2017). The current *A. petiolata* distribution ranges from southern Canada to Georgia, and from New York and Quebec west to Oregon, British Columbia and Alaska (USDA NRCS, 2017).

Long-term population trends

We established a long-term monitoring program to document local baseline population dynamics that would allow us to separate annual population fluctuations from potential future impacts of specialised biocontrol herbivores (Blossey *et al.*, 2001). Our criteria for selecting study sites included forest size > 2 ha, presence of *A. petiolata* > 3 years and protection from management (fire, herbicide, weeding or cutting) for at least 10 years. We selected 16 forested sites across northeastern North America (Fig. 1, Table 1) ranging in latitude from 39.4 to 42.7 degrees and in longitude from -74.1 to -89.2 degrees. These locations represent a transect through *A. petiolata* invasion history in North America (Nuzzo, 1993; Lankau *et al.*, 2009). Depending on location, we established sites between 2000 and 2006, and monitored them regularly for 5 to 15 years following a standardised monitoring protocol (Blossey and Nuzzo, 2003).

At each site we established 20–26 0.5 m^2 ($1 \text{ m} \times 0.5 \text{ m}$) permanent quadrats (marking corners with PVC stakes) along two to four randomly established transects. We placed the first quadrat at random in an existing *A. petiolata* patch and spaced additional quadrats at 10 m intervals. We shifted quadrat locations as necessary to ensure that *A. petiolata* rosettes or adults were present in every quadrat, except for two sites in Michigan where some quadrats did not contain *A. petiolata* at the start of the monitoring period.

At each site, we recorded data twice/year. In June or July, we recorded stem densities, stem height (cm), number of fully formed siliques on each stem, estimated percent cover of all *A. petiolata*, and estimated cover of adults and rosettes (independently, within cover classes). In September or October, we estimated rosette cover (%) and counted or estimated rosette density.

Data analyses

We standardised the time axis as date when monitoring was initiated at each site. Initial analyses indicated a nonlinear relationship between *A. petiolata* performance measures and time. Therefore, we employed generalised additive mixed models (GAMMs) to evaluate change in *A. petiolata* performance over time. Generalised additive models are a nonparametric approach that can account for nonlinear relationships through splines (Hastie and Tibshirani, 1990).

We evaluated long-term changes in adult density, June cover of adults and seedlings, mean adult stem height per quadrat, and mean number of siliques/stem/quadrat (hereafter referred to as silique number) via separate models (with Gaussian errors) applied to log-transformed (adult density, cover and silique number) or raw (stem height) data. Models

Figure 1 Location of permanent *A. petiolata* monitoring sites across eastern North America. Numbers refer to locations referenced in Table 1.

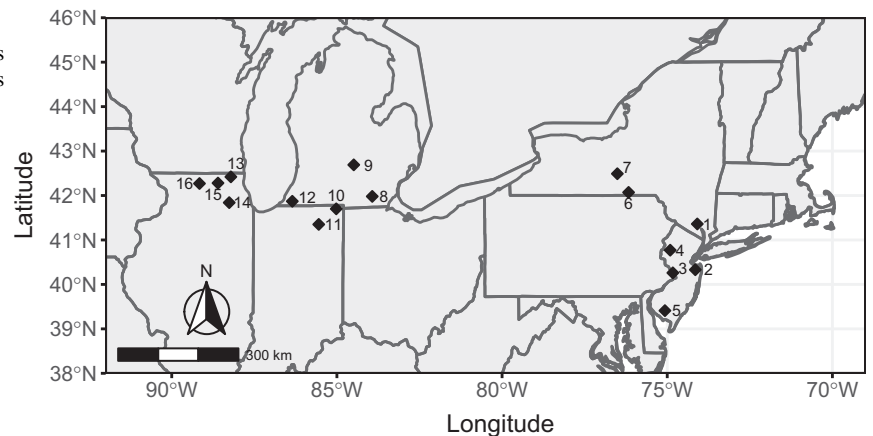


Table 1 *Alliaria petiolata* population growth rate per site over the study period ($\lambda_{\text{year.site}} = n^{\text{th}}$ root of cumulative growth rate over the study period, estimated from multi-year matrices **B** from each site, n = number of years monitored per site)

Site	State	No. years monitored	Population growth rate over the study period	95% CI
West Point	NY	12	1.125	0.973–1.365
Thompson	NJ	9	0.977	0.967–0.986
Jones	NJ	12	0.977	0.966–0.985
Point	NJ	12	1.133	0.969–1.402
Union	NJ	12	0.977	0.967–0.986
Waterman	NY	11	0.977	0.967–0.986
Leopold	NY	15	0.977	0.967–0.986
Ives Rd.	MI	6	0.977	0.967–0.986
Box Woodlot	MI	5	0.977	0.967–0.986
Pokagon	IN	12	0.978	0.968–1.019
Merry Lea	IN	12	0.977	0.966–0.986
Fernwood	MI	5	1.893	1.478–2.298
Nippersink	IL	8	1.262	0.979–1.524
Fermilab ¹	IL	10		
Marengo Ridge	IL	7	1.511	1.188–1.784
Hall Woods ¹	IL	10		

Data are means and 95% CI based on 1000 bootstrap samples. Sites are ordered East to West. Population growth rates are estimated only for time span for which demographic data are complete (missing years of data at some sites truncate the data available to estimate the growth rate) and do not necessarily reflect population size at the end of the study. Values above and below one indicate the population is projected to grow or decline respectively. Sites are ordered East to West. State two letter designations are: NY = New York; NJ = New Jersey; MI = Michigan; IN = Indiana; and IL = Illinois.

¹Fermilab and Hall Woods were not included in the matrix population analysis.

included random intercept effects for calendar year and nested effects for site and quadrat within site, as well as a random slope for monitoring year. We ran a separate GAMM model with binomial errors to evaluate changes in proportion of quadrats with *A. petiolata* presence in June.

In all models, we evaluated a smoothed function of time, fixed effects of latitude and longitude and included initial *A. petiolata* adult density as covariate. We did not test for interactions between explanatory variables. For height and silique number we also evaluated possible density dependent effects

by including adult density per quadrat. For silique number we included stem height as a covariate. We estimated smoothers with cubic regression splines (Wood, 2006). We fitted two sets of models for each performance variable. In the first set, models had a separate time smoother for each geographical region. In the second set, models had a single smoother across all sites. Residual inspection did not indicate violation of normal distribution, constant variance assumptions or auto-correlation in the data. We selected the best model based on Akaike Information Criterion (AICc) (Burnham and Anderson, 2002). We selected models using the full set of candidate models and a reduced candidate set where we identified and removed uninformative parameters following (Burnham and Anderson, 2002; Arnold, 2010). We fitted all models in R (R Core Team, 2014) using gamm4 function (Wood and Scheipl, 2017).

Matrix population model construction

We developed a linear, deterministic stage-structured matrix population model: $\mathbf{n}_t + 1 = \mathbf{A}\mathbf{n}_t$, where \mathbf{n}_t is a vector that quantifies number of individuals in each stage class at time t , and **A** is a transition matrix (Caswell, 2001). We constructed annual transition matrices **A** based on three life stages (Fig S1: seed (s), rosette (r) and adults (p) (Davis *et al.*, 2006; Kalisz *et al.*, 2014). We estimated parameter values for matrix **A** from permanent marked quadrats at each site. We estimated seedling survival (s_g) and rosette survival (s_r) by counting or estimating number of emergent seedlings per quadrat in June and number of surviving rosettes in September. We then counted number of surviving adults the following summer. We counted number of siliques produced per stem in each quadrat and estimated seed production based on average number of seeds per silique (12 seeds/silique, Nuzzo unpublished data). The monitoring protocol did not include measures of seed survival (s_s) or seed germination (g_1 and g_2), therefore we obtained estimates from an experimental seed basket study (Kalisz *et al.*, 2014) and applied those estimates to all sites and years. We averaged data across all quadrats per site to populate one matrix per year and site; therefore, sites were treated as replicates. We eliminated two sites (Fermi and Hall Woods) because of incomplete time series.

We calculated the dominant eigenvalue of each matrix to determine projected growth rates (λ). At $\lambda > 1$ populations are expected to grow; at $\lambda < 1$ declines are projected; and at $\lambda = 1$ populations are expected to remain stable (Caswell, 2000). We evaluated change in λ over the monitoring period with a Linear Mixed Model (LMM) with site as a random factor and a first order autocorrelation structure. Models evaluated second order polynomial effects of year, initial *A. petiolata* density, continental region (Northeast or Midwest) and their second order interactions. We constructed simplified models by removing one term at a time in a hierarchical fashion and retained lower-level terms if an interaction or polynomial term was included in the model. We evaluated competing models with AICc (Burnham and Anderson, 2002) and followed the same procedure as described above to remove models that appeared legitimate but were not because they contained uninformative parameters (Arnold, 2010).

We constructed multiyear projection matrices, **B**, for each study site to capture cumulative demographic trends over the study period. The matrix was estimated as the product of annual transition matrices, such that $\mathbf{B}_{\text{site}} = \mathbf{A}_{\text{site},n} \mathbf{A}_{\text{site},n-1} \dots \mathbf{A}_{\text{site},n=1}$; where $n = \text{years monitored}$ (Caswell, 2001; Kalisz *et al.*, 2014). We estimated the cumulative growth rate over the whole period (λ_c) as the dominant eigenvalue of matrix **B** and time-averaged growth rates per site ($\lambda_{\text{year.site}}$) over the study period as n^{th} root of λ_c . We constructed 95% CI based on 1000 bootstrap samples to evaluate whether $\lambda_{\text{year.site}}$ was significantly different from one.

RESULTS

When we established sites, *A. petiolata* was present in all quadrats (except in three quadrats at Box Woodlot and two at Ives Rd.). By the end of the study, *A. petiolata* frequency (proportion of quadrats containing *A. petiolata*) in June declined at 11 of 16 sites by 9% to 53%. Declines were greater at eastern sites (Fig. 2) and longitude had a significant explanatory effect (estimate \pm 1SE: -0.93 ± 0.43 , $P = 0.03$). Although two of the top three models indicated regional differences between the Northeast or Midwest, the best model (adj. $R^2 = 0.07$, AICc weight = 0.28) included a single smoother for both regions and longitude (Table S2). Models that incorporated latitude (models 4, 5, 7 and 8) had AICc values greater than the corresponding models (models 1, 2, 3 and 6) that lacked a latitude effect (Table S2). Removing this uninformative parameter rendered an AICc weight = 0.40 for the best model.

Across all sites, adult density showed large annual fluctuations but declined 48–100% from an initial mean of 13.7 ± 1.9 stems/0.5m² (mean \pm 1SE; $N = 16$ sites; range 3.62–31.05 per site) to 1.33 ± 0.4 stems/0.5m² at the end of the study, and this pattern was most obvious for sites with the longest observation periods (Fig. S2). The best performing models included initial *A. petiolata* adult density as a covariate and indicated a significant decline in adult density over time (Fig. S3) with important differences between the Northeast and Midwest (Fig. 3a and b). Sites in the Northeast showed two phases of decline, whereas at Midwest sites adult density oscillated downwards (Fig. 3a and b). Sites in the

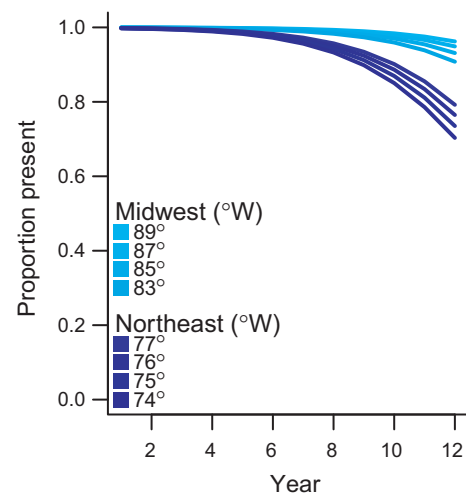


Figure 2 Proportion of quadrats with *A. petiolata* presence in June. Lines show predictions from a Generalised Additive Mixed Model with binomial errors for 0th, 25th, 50th, 75th and 100th quantiles of longitude. Model included random intercept effects for calendar year and nested effects for site and quadrat within site, as well as a random slope for monitoring year. Declines in the Northeast are more substantial than in areas in the Midwest.

Midwest were typically monitored fewer years than sites in the Northeast, increasing model uncertainty in the last years of the study. The best model of adult density (adj. $R^2 = 0.16$; AICc weight = 0.46) included initial density as a covariate (Estimate \pm 1SE: 0.17 ± 0.02 , $P < 0.001$), separate smoothers per region ($P < 0.001$), but no effect of longitude or latitude (Table S3). Models including latitude and longitude (models 2, 3, 4, 6, 7, 8) had larger AICc values than the corresponding models without these parameters (models 5, 9 and 10; Table S3). Removal of these parameters resulted in a AICc weight of 1 for the best model (Table S3).

Over time, *A. petiolata* cover (%; adults and seedlings combined) in June declined 17–98% from $29.5\% \pm 3.64$ (range 7–63% per site) at the beginning of the study to 0.5–41.3% (mean \pm 1SE) (Fig. S4). At one site (Nippersink) cover remained stable through the study period. The best model (adj. $R^2 = 0.20$; AICc weight = 0.40) included initial *A. petiolata* density (0.21 ± 0.03 , $P < 0.001$; Fig. S5), separate smoothers for Northeast and Midwest regions ($P < 0.001$) and no latitude or longitude effects (Table S4). In the Northeast, cover declined with some oscillations, but in the Midwest this pattern was less pronounced (Fig. 3c and d). Models including latitude and/or longitude had larger AICc values than corresponding models without these parameters. Removing these uninformative parameters rendered a weight of 1 for the best model (Table S4).

Average stem height per quadrat at the beginning of the study ranged from 39 to 92 cm and declined at most sites (Fig. S6). The two top models included longitude effects and indicated a decline in height over time (Table S5). Although the rate of decline differed by region in the best model ($R^2 = 0.1$; AICc weight = 0.24), it was similar for both regions in the second top model ($R^2 = 0.08$; AICc weight = 0.19) (Table S5). The best performing model indicated a

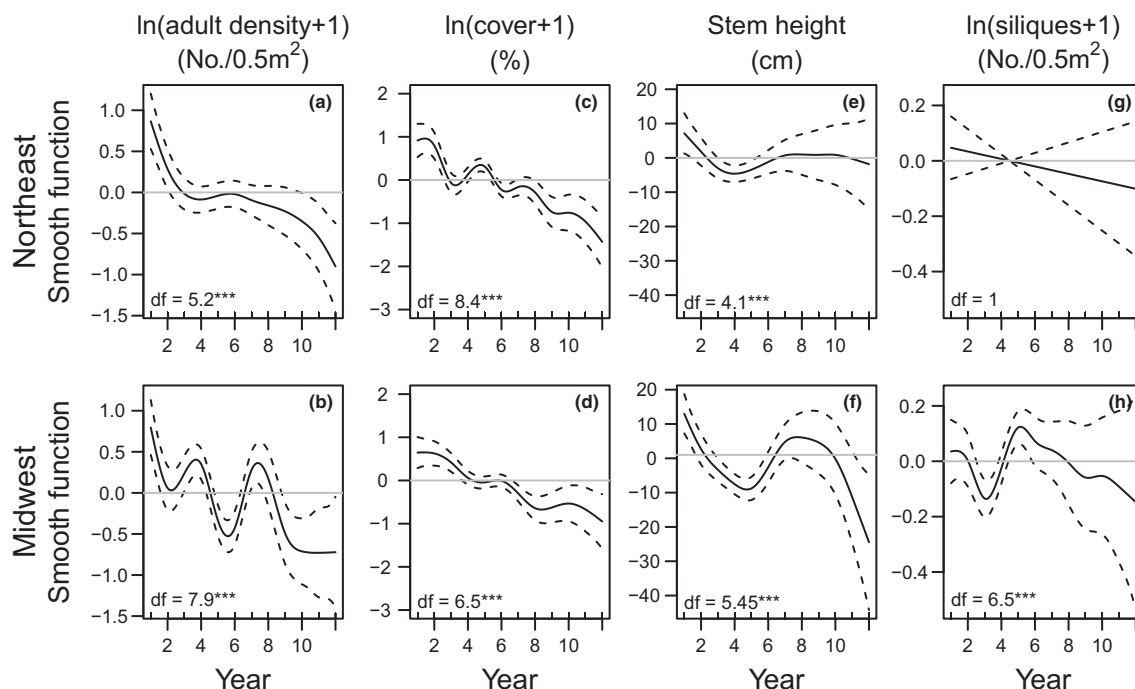


Figure 3 Generalised Additive Mixed Model smooth curves (solid lines) with 95% credible intervals (dashed lines) for *A. petiolata* adult density (number/0.5 m², log transformed, a and b), seedling and adult cover in June (% , log transformed, c and d), stem height (cm, e and f) and mean number of siliques per stem per quadrat (number/0.5 m², log transformed, g and h) in Northeast regions (top panels, $N = 7$ sites) and Midwest regions (bottom panels $N = 9$ sites; see Table S1 for site designation). Locations with zero stem density were excluded from analyses of stem height and number of siliques. Models included random intercept effects for calendar year and nested effects for site and quadrat within site, as well as a random slope for monitoring year. Note different y-axis scales for different performance measures. df = degrees of freedom; *** $P < 0.001$.

decline in stem height in the Midwest, whereas in the Northeast stem height decreased in the first years of the study and then remained stable (Fig. 3e and f). Stem height significantly decreased with longitude (-6.57 ± 2.96 , $P = 0.03$; with taller stems at western sites, Fig. S7) but was not significantly correlated with initial *A. petiolata* adult density or latitude (Table S5). Removing models with latitude and/or initial density (uninformative parameters) from the set resulted in AICc weight = 0.46 and 0.35 for the two top models respectively.

Silique production/stem remained relatively stable at most sites throughout the study period (5.7–22.8 siliques/stem at study initiation) (Fig. 3, Fig. S8). All best models included a smoother per region, an interaction between stem height and adult density and longitude and latitude effects. The best model (adj. $R^2 = 0.8$, AICc weight = 0.53; Table S6), indicated mean silique number per stem per quadrat decreased in the Midwest but did not change in the Northeast. Silique production was positively correlated with stem height (estimate \pm 1SE: 0.03 ± 0.0007 , $P < 0.001$) and adult density (0.06 ± 0.02 , $P = 0.002$), with taller stems in quadrats with low stem densities producing more siliques than stems of the same height in quadrats with high stem densities (Fig. 4). Silique production was negatively correlated with latitude (-0.17 ± 0.04 , $P < 0.001$) and longitude (-0.13 ± 0.5 , $P = 0.007$), with stems at northern and eastern sites producing more siliques than stems at southern and western sites (Fig. 3, Fig. S9). Initial *A. petiolata* density was not included as covariate in the best model and its addition resulted in lower

AICc values than the corresponding model without initial density (Table S6). Removing this model from the candidate set resulted in an AICc weight of 0.80 for the best model.

Demographic analysis

At the beginning of our study, projected site-specific population growth rates (1.33 - 1.85; mean \pm 1SE: 1.56 ± 0.04) indicated expanding populations. However, population growth rates significantly decreased over time (Table S7; Fig 5) at all sites (Fig. S10). Analysed over the whole study period, the time-averaged growth rate per site ($\lambda_{\text{year.site}}$) was significantly less than one at eight sites, did not differ from one at four sites and was significantly higher than one at two sites (Table 1). Estimates assume that seed survival and germination are similar across sites and did not vary over time.

DISCUSSION

The results of our regional investigation require us to reject our first assumption—*A. petiolata* is unable to maintain stable or increasing populations over time. While our monitoring protocol was not intended to capture very early stages of arrival at a site, our data suggest an initial local abundance increase, followed by sustained vigour declines. Earlier demographic models developed to aid in selection of potential bio-control agents for *A. petiolata* identified transitions from rosettes to flowering plants as most important in *A. petiolata*

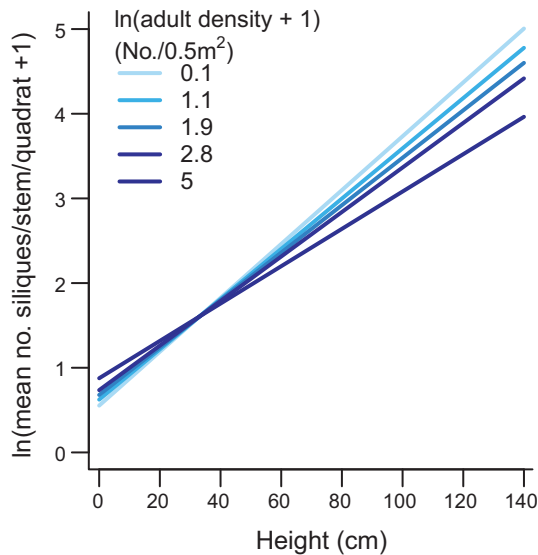


Figure 4 Number of *A. petiolata* siliques per stem as a function of stem height (cm) and adult density (number/0.5 m², log transformed). Lines depict model predictions averaged across all study sites and years for mean latitude (41.57) and longitude (−81.58) and for 0th, 25th, 50th, 75th and 100th quantiles of log-transformed adult density (number/0.5 m²). Model included random intercept effects for calendar year and nested effects for site and quadrat within site, as well as a random slope for monitoring year. Darker colours indicate higher adult density (log-transformed).

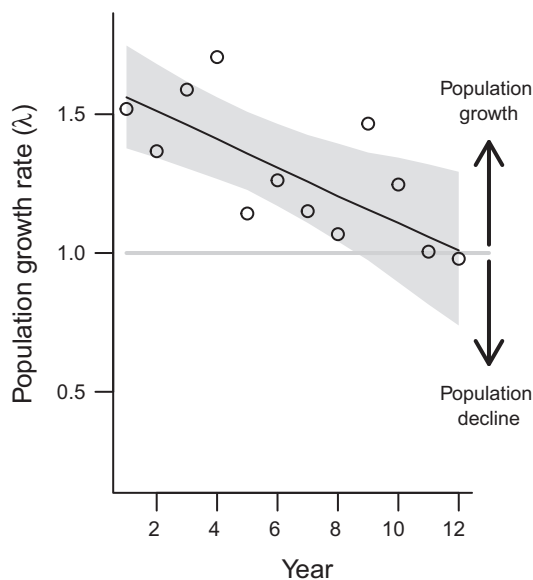


Figure 5 Population growth rate of *A. petiolata* over time. Points represent mean growth rate across sites, lines and shaded areas represent marginal means and 95% CI based on linear mixed model predictions ($N = 1000$ bootstrap samples). Population growth rates are estimated only for time spans for which demographic data are complete (missing years of data at some sites truncate the data available to estimate growth rates) and do not necessarily reflect population size at the end of the study. Values above and below one indicate the population is projected to grow or decline respectively. Model included random intercept effects for site.

demography (Davis *et al.*, 2006; Evans *et al.*, 2012). This is exactly what we document and, despite abundant germination and a fairly long-lived (10–13 years) seedbank (Blossey *et al.*, 2017), over time projected population growth rates decline to <1 . This phenomenon is not restricted to our long-term monitoring sites and has been noted observationally or through demography investigations by others (Kalisz *et al.*, 2014; Dávalos *et al.*, 2015b; Faison *et al.*, 2019), but we are the first to document and quantify these declines through a chronosequence at many different locations.

We find support for our second prediction that local declines are a function of regional residence time. The species first established in the East and then spread into the Midwest (Nuzzo, 1993) and our data indicate that *A. petiolata* declines occurred faster and were more pronounced at eastern study locations (Fig. 1). Although detailed mechanisms responsible for these findings remain elusive at present, unique regional climates, soil and vegetation characteristics may be important in determining local site trajectories. However, longer overall residence time in the East may also facilitate and enhance local build-up of biotic resistance, or other eco-evolutionary feedbacks. While we did encounter above ground natural enemies (herbivores or diseases), they never appeared abundant enough to strongly affect *A. petiolata* populations. Instead, the patterns we describe are consistent with expectations of plant-soil feedback (PSF), where plant species-specific rapid soil conditioning leads to performance reductions (negative soil feedback) (Klironomos, 2002; Bever *et al.*, 2010; van der Putten *et al.*, 2013). The role of PSF in structuring plant communities (Bennett *et al.*, 2017) and the importance in range expansion or biological invasions is now well established (Koorem *et al.*, 2020; Wolfe and Klironomos, 2005; Reinhart and Callaway, 2006) but how these impacts change over time is far less clear.

Ecological dominance waning over 100–300 years associated with negative soil feedback are described for introduced plants in New Zealand (Diez *et al.*, 2010) and they may play a role in the reduction in abundance of invasive plant species described for eastern North America (Warren *et al.*, 2019). We have some evidence suggesting the importance of negative soil feedback in affecting survival and vigour of *A. petiolata* from a site in central New York. At this location, which is not part of our long-term monitoring, we were able to observe a detailed chronosequence of *A. petiolata* arrival, spread and decline over a 10-year period (for details see Plant-Soil Feedback section in Supplementary Material). Our preliminary experiments from this single location leads to a new hypothesis: the decline of *A. petiolata* as a function of local residence time, is caused by negative soil feedback. PSF may also help explain the regional differences between eastern and western sites. For example, legacy effects of differences in precipitation (Crawford & Hawkes, 2020) or previous land use histories that create persistent different microbial communities can affect plant demography and persist from decades to centuries (Wubs *et al.*, 2019).

We need additional mechanistic work to assess whether similar processes occur in other regions throughout the range of *A. petiolata* in North America. We were unable to link a chronosequence to population trends at our long-term sites

because we established quadrats after the initial colonisation phase had occurred. In addition, the small-scale patch dynamics described as advance and retreat (Nuzzo, 1999) and the potential for long-lasting legacy effects (Bezemer *et al.*, 2019) may lead to erroneous conclusions. But because abundance and vigour declines are a function of local residence times and small-scale patch dynamics (at the order of a few m), a perplexing local and regional invasion dynamic emerges. At invaded sites *A. petiolata* abundance typically initially increases with some annual fluctuations and patchy spread through a site. The areas first occupied then go through a prolonged phase of decline until λ is reduced to <1 , whereas at the same time *A. petiolata* populations at the invasion fronts are rapidly expanding. The continued availability of previously unoccupied areas allows *A. petiolata* to spread regionally and across the continent. This is likely to continue, although only areas already invaded by introduced earthworms appear to allow *A. petiolata* invasions, (Nuzzo *et al.*, 2009), thus limiting available habitat the species may be able to colonise in North America. The potentially available habitat for expansion of *A. petiolata* continually shrinks as once occupied patches become inhospitable, at least for establishment and maintenance of large populations. Although we also do not know how long this biotic resistance may last (but see Bezemer *et al.*, 2019). Furthermore, rapid evolutionary changes in the invader and the invaded lead to a reduction in *A. petiolata* impact as a function of residence time (Lankau *et al.*, 2009; Lankau, 2012a; Lankau *et al.*, 2014).

Our data were collected in areas with the oldest invasion history of *A. petiolata* in North America (Nuzzo, 1993; Lankau *et al.*, 2009) with unique regional climate, soil and vegetation characteristics. The species has since spread more widely triggering continued widespread manual and chemical removal experiments. We have no information on the long-term population dynamics in areas outside of our investigation, but we only detected long-term declines because we required cessation of *A. petiolata* management for the duration of our study. Removal of *A. petiolata* may in fact set back negative soil feedback or other processes that collectively lead to population declines. It appears important that local management efforts are cognizant of the possibility that their activities may be detrimental to *A. petiolata* declines and local plant community recovery. We recommend for local managers to set aside certain locations for observational investigations to assess whether the phenomena we describe occur outside of our region.

Arrival and spread of *A. petiolata* into local ecosystems that continue to lose their diversity worries land managers, as they assume a cause-and-effect relationship. The species certainly has a potent arsenal of secondary chemistry (Callaway *et al.*, 2008; Lankau, 2011a) that may affect many biota; however, effects reported by some (Roberts and Anderson, 2001; Stinson *et al.*, 2006; Wolfe *et al.*, 2008; Barto *et al.*, 2011; Hale *et al.*, 2011; Bialic-Murphy *et al.* 2019) do not materialise in other studies (Dávalos and Blossey, 2004; Burke, 2008; Burke and Chan, 2010; Lankau, 2010; Wixted and McGraw, 2010; Ivanov and Keiper, 2011; Koch *et al.*, 2011; Hahn and Dornbush, 2012; Lankau, 2012b). Decadal dynamics we describe further complicate *A. petiolata* impact assessments, which need to be separated from impacts of other stressors, such as

white-tailed deer (*Odocoileus virginianus*) and invasive earthworms (Didham *et al.*, 2007; Dávalos *et al.*, 2014, 2015a, b; Frelich *et al.*, 2019). Few such studies exist (Waller and Maas, 2013; Dávalos *et al.*, 2014, 2015a, b, c; Nuzzo *et al.*, 2017) but future study designs, as well as interpretation of existing data need to be cognizant of presence and importance of other stressors and the possibility of *A. petiolata* invasion and decline that occur over a decadal timeframe. This limits the ability of short-term experiments to capture long-term impacts in the field and calls for more longitudinal research.

Our work contributes to the increasing body of evidence for declines in invasiveness and therefore potential ecological impacts of introduced species across many different taxa. Rapid evolutionary changes allowed *A. petiolata* to thrive in North America (Lankau, 2011b) but rapid eco-evolutionary feedback in native species has reduced ecological and evolutionary novelty and initial negative impacts (Hierro and Callaway, 2003; Callaway *et al.*, 2008; Mangla *et al.*, 2008; Wolfe *et al.*, 2008) and we show widespread declining *A. petiolata* population growth rates. These phenomena have important implications for how we approach research in and management of biological invasions. If impacts are caused by *A. petiolata*, how quickly do impacts materialise, do they persist, or do they fade (Lankau, 2012b) once the initial high abundances are reduced? Do affected species or communities recover over time, and how quickly? Does active management of garlic mustard extend local dominance potentially increasing impacts?

Build-up of native natural enemies (including diseases and parasites) that affect species demography appear common in documented declines (Carlsson *et al.*, 2009; Diez *et al.*, 2010; Ross *et al.*, 2010; Faillace *et al.*, 2017; Gerard *et al.*, 2018). This biotic resistance may be a widespread but unrecognised phenomenon for many species that naturalise but never become invasive, and therefore escape scientific or management focus. We believe it is critically important for scientists to embrace use of better and long-term assessment protocols to ascertain demography of naturalising or introduced species. We recognise logistical and financial difficulties of such approaches, but also opportunities for advanced collaborative manager-research scientist partnerships. Using a standardised monitoring approach offers one possible example but there are many others that need to be developed to capture the potential for waxing and waning in invasive species, similar to patterns we describe for *A. petiolata*.

Where large plant populations exist and eradication is no longer an option, we recommend establishing long-term 'research refuges' to allow evaluation of eco-evolutionary processes and potential buildup of local biotic resistance or biological control by native organisms to occur over time in absence of management. This switch in scientific focus from potential traits of invaders, to assessing biotic resistance traits of invaded communities may lead to improved understanding of invasion dynamics.

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AUTHOR CONTRIBUTIONS

BB and VN conceived the idea and developed the long-term monitoring protocol. All authors contributed to data collection. VN collated and proofed all data, AD analysed the data, BB led the writing and all authors contributed to the final version.

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DATA AVAILABILITY STATEMENT

The data are available in Dryad (<https://doi.org/10.5061/dryad.mpg4f4qxh>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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