In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives

Susan Kalisz[a,1], Rachel B. Spigler[a,2], and Carol C. Horvitz[b]

[a]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260; and [b]Department of Biology, University of Miami, Coral Gables, FL 33124

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A major goal in ecology is to understand mechanisms that increase invasion success of exotic species. A recent hypothesis implicates altered species interactions resulting from ungulate herbivore overabundance as a key cause of exotic plant domination. To test this hypothesis, we maintained an experimental demography deer exclusion study for 6 y in a forest where the native ungulate *Odocoileus virginianus* (white-tailed deer) is overabundant and *Alliaria petiolata* (garlic mustard) is aggressively invading. Because population growth is multiplicative across time, we introduce metrics that correctly integrate experimental effects across treatment years, the cumulative population growth rate, λ_c, and its geometric mean, $\lambda_{per\text{-}year}$, the time-averaged annual population growth rate. We determined λ_c and $\lambda_{per\text{-}year}$ of the invader and of a common native, *Trillium erectum*. Our results conclusively demonstrate that deer are required for the success of *Alliaria*; its projected population trajectory shifted from explosive growth in the presence of deer ($\lambda_{per\text{-}year}$ = 1.33) to decline toward extinction where deer are excluded ($\lambda_{per\text{-}year}$ = 0.88). In contrast, *Trillium*'s $\lambda_{per\text{-}year}$ was suppressed in the presence of deer relative to deer exclusion ($\lambda_{per\text{-}year}$ = 1.04 vs. 1.20, respectively). Retrospective sensitivity analyses revealed that the largest negative effect of deer exclusion on *Alliaria* came from rosette transitions, whereas the largest positive effect on *Trillium* came from reproductive transitions. Deer exclusion lowered *Alliaria* density while increasing *Trillium* density. Our results provide definitive experimental support that interactions with overabundant ungulates enhance demographic success of invaders and depress natives' success, with broad implications for biodiversity and ecosystem function worldwide.

life table response experiment | herbivory | biotic resistance | temperate deciduous forest conservation | forest understory herbs

Steadily increasing pressure by invasive plant species on native biodiversity (1) disrupts both community and ecosystem function (2) and results in staggering economic costs worldwide (3, 4). A major goal in ecology is to understand how changes over time in species interactions affect invasion success of exotic species (5–8). According to ecological theory, the ability of the resident community to limit the success of invading exotics [biotic resistance (9, 10)] will depend upon ecological context that includes the suite of local interactors (11–15). The abundance of herbivores and their local impacts (11, 14, 16) can play a prominent role in how fast plant populations grow or shrink and how much the relative abundance of plant species changes over time (5, 15), including changes associated with plant invasions (11, 16–19). Recently, increased browsing pressure by overabundant ungulate herbivores on native plant communities has been proposed as a fundamental cause of a shift from native to exotic plant domination in forests and rangelands worldwide (11, 16, 20). Wild and domesticated ungulates (e.g., deer, elk, goats, sheep, horses, cows) that are either native or introduced have all been implicated in this process (11, 16, 20).

Overabundant ungulates may change the success of invading exotics in numerous ways. Ungulate browsing on natives may depress their abundance and ability to compete (21–24) and increase abiotic resources available to invaders (11, 25, 26), which can act synergistically to decrease communities' ability to resist invasion (biotic resistance; refs. 8 and 10). Ungulates disperse exotic seeds (27, 28) and create novel abiotic conditions with respect to soil disturbance, soil quality, and light availability (21, 22, 26), which may enhance exotic establishment and growth. Moreover, although ungulates are considered diet generalists, in fact, they frequently behave as selective foragers (21–24, 29), preferring natives to exotics. In this circumstance, unpalatable invaders can have a double advantage over natives—both release from historic enemies (20) and inedible to new potential enemies in the invaded range (30, 31). Together, these mechanisms not only implicate overabundant ungulates in their direct impact on the rate at which populations of palatable native species grow or shrink, but point to their potentially pivotal role in reducing the biotic resistance of the native community to favor invaders (13, 14).

To determine how ungulate herbivores affect the fitness of invaders and natives, field experiments that manipulate herbivore access for several years and are spatially well replicated are required (11, 32, 33). The multiyear, population-level demographic data gained in such experiments can be used to estimate the ultimate metric of fitness: population growth rate (λ). However, despite the widespread use of manipulative experiments that alter herbivore access to plants, we still lack appropriate demographic data (i.e., complete schedules of fertility, mortality and growth

ECOLOGY

Significance

In ecosystems worldwide, the presence of overabundant ungulates (e.g. deer, cows) and the invasion of exotic plants are disrupting native communities. A recent hypothesis causally links these problems implicating overabundant ungulates in enhancing invaders' demographic success. We tested this hypothesis in a forest where white-tailed deer are overabundant and garlic mustard is aggressively invading. Using long-term, replicated deer exclusion/deer access plot pairs, we quantified population density, growth, and decline of this invader and native plants. We conclusively demonstrate that deer are required for garlic mustard success; its local extinction is projected where deer are absent. Our findings provide the first definitive support connecting overabundant ungulates to enhanced invader success, with broad implications for biodiversity and ecosystem function.

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Data deposition: The data, including annual population projection matrices and table of weightings for spatial averages, have been deposited with DRYAD, www.datadryad.org (10.5061/dryad.bk272).

[1]To whom correspondence should be addressed. E-mail: kalisz@pitt.edu.

[2]Present address: Department of Biology, Temple University, Philadelphia, PA 19122.

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for all stages) in invaded systems (2, 14, 17, 32, 33). Instead, herbivore–plant invader experiments typically report simple metrics of plant success (e.g., percent cover or counts of individuals) at a single time point. For example, the metric "percent cover" estimates the total leaf area of a species, often relative to other species. Lower leaf area of native plants where ungulates have access could merely be the result of leaf tissue lost to herbivory, with no actual change in invader or native numbers. Likewise, "snapshot counts" of invaders often leave out critical life cycle stages and do not provide information on rates of survival, reproduction, or growth, without which population dynamics cannot be analyzed. Thus, it is not surprising that ungulate exclusion experiments that apply such metrics provide no unified answer regarding exotic invaders [effect on invasion success: none (34–36); mixed (37, 38); positive (39–41; reviewed in ref. 16)] because these studies cannot address population viability of invaders or natives. Also, although evidence of ungulates' influence on native plant population dynamics from exclusion experiments has been previously demonstrated (e.g., refs. 42 and 43), our study is distinct. We know of no other such experiments testing the link between ungulates and invasive exotic population growth rate in invaded systems.

Here, we use experimental demography and stage-based data (rates of survival, fertility, and growth) collected over multiple years to test the hypothesis that an overabundant native ungulate herbivore drives positive population growth of invaders (11, 16). We emphasize that in herbivore removal experiments the fitness of plant populations, which is measured by population growth rate, is predicted to rebound with persistent, multiplicative beneficial effects over time. What has not previously been recognized in such experiments is that treatment effects accumulate over the span of an experiment (44), necessitating a quantitative metric that integrates fitness over the entire life cycle and over time. Moreover, population growth is a process that is multiplicative across time. Thus, we introduce the use of cumulative population growth rate, λ_c, at the end of a multiyear experiment as the metric that correctly integrates experimental effects across the observed sequence of demographic changes across time. Our multiyear demographic projection and the corresponding multiyear retrospective sensitivity analysis provide fresh insights. To facilitate comparisons of our results with studies that estimate λ from single-year transitions, we present $\lambda_{per\text{-}year}$, the geometric mean of λ_c. Our retrospective sensitivity analyses [similar to life table response experiment analysis for periodic matrices (45, 46)] of λ_c reveal how each part of the life cycle contributes to overall differences in cumulative population dynamics caused by an experimental manipulation. We conclusively show that overabundant deer create conditions favorable for explosive exponential population growth of an exotic plant invader, but that when deer are excluded, populations of the invader are projected to decline exponentially.

We focus on the native ungulate *Odocoileus virginianus* (white-tailed deer; hereafter, deer) and the exotic herbaceous understory invader *Alliaria petiolata* (Brassicaceae; garlic mustard; hereafter, *Alliaria*), which both present serious management concerns in North American forests. Relative to historical records, deer densities are currently 4–10 times higher than pre-European settlement densities across North America (47). Overabundant native deer in forests exert the same kinds of pressures as other ungulates (native and nonnative, wild and domesticated) globally, including perturbation of understory communities (22, 27, 39), exotic seed dispersal (27), and alteration of abiotic conditions (21, 39). Likewise, *Alliaria* ranks among the most problematic forest invaders in North America (48). Introduced by early colonists, it was naturalized on Long Island, New York, by 1868 (reviewed in ref. 48). In its native Eurasia, *Alliaria* grows in edge or disturbed habitats, whereas in North America it increasingly occupies forest interiors (48). Relative to the slow-growing, long-lived understory community it invades, *Alliaria* has a rapid, biennial life cycle: spring seedlings form overwintering rosettes by autumn. In their second year, plants reproduce, disperse seeds, and die. In its invaded range, *Alliaria* has high population growth rates (λ = 1.4–3.4) (48), which project annual increases in numbers of 40–240%. *Alliaria*'s invasive success has been hypothesized to result from various factors. These include the following: novel allelopathic weapons, enemy release, positive soil feedback, taxonomic novelty, high competitive ability, and specific phenotypic traits. No single factor has yet to explain the broad reach of this tenacious exotic (reviewed in ref. 48). Here, we investigate what has not been previously explored: the role of ungulate disruption of native community biotic resistance (13) on *Alliaria*'s invasion success. To date, deer and *Alliaria* have been foci of intense, largely separate, research efforts. Our approach uses experimental demography to jointly examine these two issues. Together, they constitute an ideal system to investigate ungulate–exotic plant invasion linkages (11, 16).

Our experiment was conducted in a beech–maple forest in southwestern Pennsylvania (Trillium Trail Nature Reserve, Allegheny County, Pennsylvania: 40° 52′ 01.40″ N; 79° 90″ 10.75″ W). Winter aerial flyovers of this area performed between 1993–2004 revealed overabundant deer: currently 20–42 deer per km^2 compared with an historic density of 10–12 deer per km^2 (Fig. S1). In a different area in this same forest, Knight et al. (39) used an indirect metric of plant performance and found that relative percent cover of *Alliaria* was lower and that there was significantly less bare ground where deer were excluded relative to sites where deer were present (39). However, in that study *Alliaria* nevertheless remained abundant (the second most abundant species) even where deer were excluded. That study (39), which used relative percent cover as a response metric, left several questions unanswered, including the following: Was *Alliaria*'s relative decline due to the native species increasing in cover with no actual change in cover of the invader? Did the tenacious invader's population growth rate actually decline? Given these unanswered questions from the earlier study, the Trillium Trail forest was an ideal location to address these questions and to conduct a definitive demographic experiment that could distinguish among these mechanisms. In 2002, we established paired plots (n = 6 pairs of 14 × 14-m plots) with one plot per pair randomly assigned to a fenced treatment that excluded deer (see *Materials and Methods* for details). The other plot in each pair remained unfenced and experienced ambient levels of deer and other animals. We compared population-level responses of native understory herbaceous perennial species and *Alliaria* between treatments for 6 y. For three focal native herbs that are palatable to deer (e.g., ref. 49) and the unpalatable *Alliaria*, we quantified reproductive success each year. For *Alliaria* and one of the natives, *Trillium erectum* (Melanthiaceae, hereafter *Trillium*), we additionally quantified the complete schedule of survival, fertility, and growth rates each year. We selected *Trillium* as a counterpoint to *Alliaria* as it is the most common flowering herbaceous species found at Trillium Trail Nature Reserve. Moreover, *Trillium* species are a preferred food source for deer (49) and well-known phytoindicators of deer browse (e.g., ref. 49; but see ref. 50). In a nonexperimental study, deer browse levels within a population were negatively correlated with population growth rate for another species in the genus, *Trillium grandiflorum* (51). Accordingly, *Trillium* represents a model for understanding the impact of deer on native species, and the loss of such browse-sensitive species can be a metric of decline in forest integrity (52). We predicted that, if ungulates disrupt the native community and enhance exotic invasion success, then in plots experimentally protected from deer: (*i*) native species would have higher reproductive success, (*ii*) *Trillium* fitness would increase and its density would increase, (*iii*) *Alliaria* fitness would decrease and its density would decline. Meanwhile, in plots where deer were allowed access, we expected either the opposite trends or no change from initial conditions. Alternatively, if any of the other previously hypothesized mechanisms for *Alliaria*'s success (e.g., novel weapons, enemy release) are at play and more important than herbivore impacts, then we would expect

Alliaria's population growth rate to remain high despite deer exclusion, while predictions for the effects of deer on the natives remain the same.

In brief, from 2003 to 2008 at annual censuses, we scored reproduction and survival of individuals of *Alliaria* and of the three native perennials that are preferred food sources for deer (49): *Trillium*, *Maianthemum racemosum* (Ruscaceae), and *Polygonatum biflorum* (Ruscaceae). In plots accessible to deer, we also scored deer browse. To assess the effect of deer exclusion on the fitness of *Trillium* and *Alliaria*, we implemented our multiyear matrix projection analysis to calculate cumulative population growth rates from 2003 to 2007 for each treatment. To construct matrices, we defined five life cycle stages for the perennial *Trillium* (germinant bank, seedling, one-leafed juvenile, three-leafed nonflowering, and three-leafed flowering; Fig. S2*A*) and three life cycle stages for *Alliaria* (dormant seed in the seed bank, rosette, and fruiting adult; Fig. S3*A*). Matrix elements were calculated as a function of the vital rates associated with each stage transition (Figs. S2*A* and S3*A*). We captured cumulative effects of deer exclusion or continued deer overabundance over time, parameterizing multiyear projection matrix models **B**, for each species and treatment by multiplication of annual projection matrices $\mathbf{A}_{\text{YEAR-TREATMENT}}$ (e.g., $\mathbf{B}_{\text{DEER}} = \mathbf{A}_{\text{2006-DEER}}\,\mathbf{A}_{\text{2005-DEER}}\,\mathbf{A}_{\text{2004-DEER}}\,\mathbf{A}_{\text{2003-DEER}}$). The matrix **B**, at the heart our analyses, contains the rates at which individuals that were at a given stage at the beginning of the experiment will have either become or produced individuals of each stage after four transition years. Our analyses of multiyear matrices provide integrative measures of plant fitness over the time frame of the experiment, including treatment-specific cumulative population growth rates (λ_c, the dominant eigenvalue of **B**), time-averaged λ's ($\lambda_{\textit{per-year}\text{-TREATMENT}}$ = the fourth root of the dominant eigenvalue, λ_c, of **B**), and an overall measure of the effect of protecting plants from deer on plant fitness $\Delta\lambda_{\textit{per-year}} = \lambda_{\textit{per-year}\text{-NO_DEER}} - \lambda_{\textit{per-year}\text{-DEER}}$. [Note: Pooled plot data (*Trillium*) and individual plot data (*Alliaria*) were used. See *Materials and Methods*, *Matrix Construction for Each Species and Treatment*.] Finally, to uncover mechanistic differences between the response of the native and the exotic to deer exclusion, we use a life table response experiment retrospective sensitivity analysis (45, 46). The analysis shows how important each of these 4-y demographic rates is to differences in λ_c between treatments, quantified by contributions made during transitions from stage *j* to stage *i*, c_{ij}.

Results

Over the course of the experiment, 2003–2008, we collected data on >9,000 individually tagged plants in six paired plots. In plots where deer had access, they browsed an average of 22% (±0.08 SD) of the palatable native individuals per year (n = 6 y), with dramatic consequences for reproduction of all three species (Fig. 1). At the start of the experiment, only 2–3% of the natives were reproductive in either treatment, but beginning in 2004, the percentage of native individuals that reproduced in the plots protected from deer increased dramatically (Fig. 1*B*). In contrast, this percentage remained low where deer had continual access. By 2008, 26% of natives in plots protected from deer successfully reproduced compared with only 5% where deer had continuous access (G statistic = 254.7, P < 0.00001). These results demonstrate large negative effects of deer on the reproductive capacity of the natives.

The restoration of reproduction in plots where deer were excluded translated into significant increases in the population-level fitness of the native *Trillium*. In the plots protected from deer, the *Trillium* population is projected to increase 20% annually [$\lambda_{\textit{per-year}\text{-NO_DEER}}$ = 1.20; 95% confidence interval (CI): 1.18–1.22; n = 5,000 bootstrap samples]. In the plots where deer were allowed access, population growth was substantially lower ($\lambda_{\textit{per-year}\text{-DEER}}$ = 1.04; 95% CI: 1.03–1.06; n = 5,000 bootstrap samples). A permutation test comparing the two treatments' $\lambda_{\textit{per-year}}$ revealed that the overall improvement in *Trillium*'s fitness

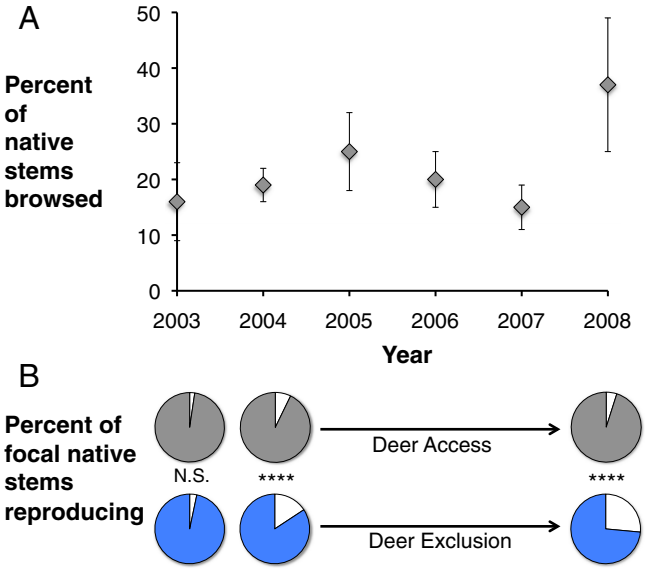

Fig. 1. (*A*) Annual average percentage (±SEM) of focal native perennial understory herbs browsed by deer in plots (n = 5) that were accessible to deer between 2003 and 2008 (focal species: *Trillium erectum*, *Polygonatum biflorum*, and *Maianthemum racemosum*). (*B*) The percentage of individuals (of the three focal native species) that successfully reproduced (produced fruits, shown in white) did not differ significantly between treatments at the start of the experiment (2003: G statistic = 1.7, P = 0.19, N_{DEER} = 1,021, $N_{\text{NO_DEER}}$ = 1,031) but was significantly higher in deer exclusion plots than deer access plots in all subsequent years (2004: G statistic = 41.4, N_{DEER} = 1,009, $N_{\text{NO_DEER}}$ = 1,163; 2005: G statistic = 100.4, N_{DEER} = 1,204, $N_{\text{NO_DEER}}$ = 1,253; 2006: G statistic = 46.3, N_{DEER} = 1,105, $N_{\text{NO_DEER}}$ = 1,096; 2007: G statistic = 131.5, N_{DEER} = 1,272, $N_{\text{NO_DEER}}$ = 1,546; 2008: G statistic = 254.7, N_{DEER} = 1,201, $N_{\text{NO_DEER}}$ = 1,613; 2004–2008, all P < 0.00001; $N_{\text{TREATMENT}}$ = total number of focal natives in a treatment each year).

due to its protection from deer, $\Delta\lambda_{\textit{per-year}} = 0.16$, is significant ($P$ = 0.0002; n = 5,000 permutations). Our retrospective sensitivity analysis (45) clearly shows that differences between treatments in the demographic rates of the flowering stage made the greatest contribution to the differences in population growth rate between the treatments (Fig. 2*A*). Protection from deer over the course of the experiment resulted in flowering plants with a higher probability of remaining reproductive and a lower probability of becoming nonflowering over this period. Similarly, nonflowering plants had a higher probability of becoming reproductive and a lower probability of remaining nonreproductive (Fig. 2*A*). These effects combine to generate significantly higher population growth where deer were excluded. The effect of deer on *Trillium*'s projected population growth mirrors the change in actual *Trillium* abundance seen across the study period in the two treatments (Fig. 3).

In contrast, deer never browsed *Alliaria* in our experimental plots. In fact, the presence of deer ensures *Alliaria*'s high population growth rate and high density. At the start of our experiment, *Alliaria* was increasing in both treatments, and its fitness did not differ significantly between the treatments: $\lambda_{\text{2003-DEER}}$ = 1.11 (SEM = 0.07) vs. $\lambda_{\text{2003-NO_DEER}}$ = 1.28 (SEM = 0.14) (Fig. 4*A*). However, *Alliaria*'s population growth rate diverged dramatically between treatments by the end of the experiment. Where deer had continuous access, fitness over the duration of the experiment remained high and not significantly different from the start of the experiment ($\lambda_{\textit{per-year}\text{-DEER}}$ = 1.33, SEM = 0.11; Fig. 4*A*). Conversely, in the plots protected from deer, fitness declined by ~40% relative to the start of the experiment ($\lambda_{\textit{per-year}\text{-NO_DEER}}$ = 0.88, SEM = 0.09; Fig. 4*A*) and was significantly less than 1.0. Thus, we found a large, negative fitness difference due to long-term protection from deer, $\Delta\lambda_{\textit{per-year}} = -0.45$. Overall, where deer are present, *Alliaria* populations are

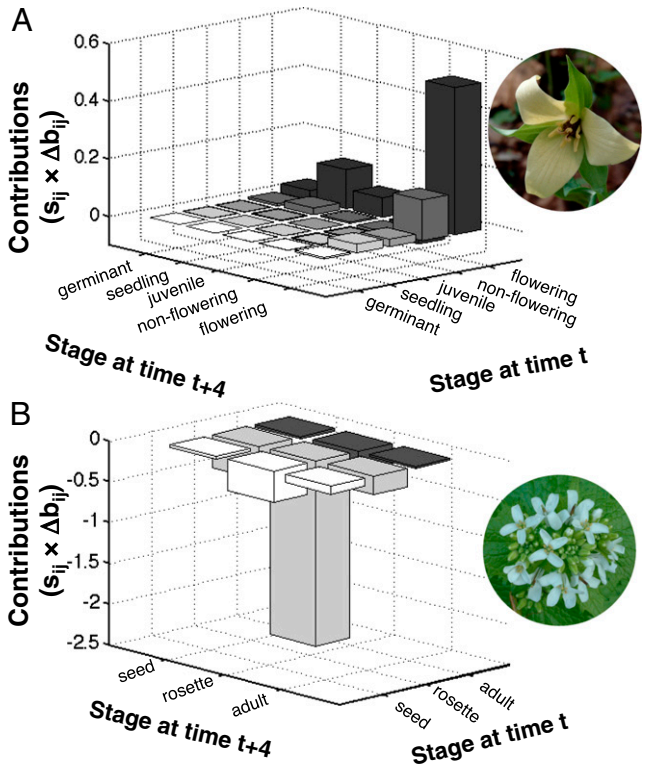

Fig. 2. Our application of a multiyear retrospective sensitivity analysis [life table response experiment analysis; see text for details (46)] shows how different life cycle transitions and rates contributed to the difference in cumulative 4-y population growth rate (λ_c) between the treatments (deer excluded vs. deer access) for (*A*) the native *Trillium erectum* and (*B*) the exotic *Alliaria petiolata*. Deer exclusion had a positive effect on all stages of *Trillium* (*A*). The largest positive contribution (c_{ij}) involves the reproductive stage. In contrast, the consistently negative contribution values (*B*) indicate that deer exclusion negatively affected all stages of *Alliaria*. The largest negative contribution involves rosette-stage transitions.

increasing ~30% annually, but in plots protected from deer they are declining ~12% annually and if conditions remain the same will eventually go extinct, according to model projections. The initial spatially weighted mean population density in the deer exclusion plots was 8.9 adults per m^2. Our projection indicates the extinction threshold (defined conservatively as a density of 0.005 adults per m^2, <1 individual within each 14 × 14-m plot) would be reached after 58.6-y. Our annual field censuses corroborate the projected decline. Over the course of the experiment, *Alliaria* adult density in plots protected from deer declined 58% but did not decline in plots where deer had access (Fig. 4*B*). Our retrospective sensitivity analysis shows that the rate at which rosettes at the beginning of the experiment have produced rosettes after 4 y is the most important of these 4-y demographic rates for *Alliaria* (Fig. 2*B*). We emphasize that many processes (survival, growth, and reproduction) across seasons and across years are multiplicative components of this 4-y rosette-to-rosette rate. All aspects of the invaders' life cycle are stifled where plants are protected from deer, because every matrix element made negative contributions to the difference in λ_c between treatments (Fig. 2*B*). This result is in stark contrast to the positive effects of the contributions in *Trillium* when plants are protected from deer (Fig. 2*B*).

Discussion

Our results conclusively link *Alliaria*'s invasion success to the presence of an overabundant native ungulate, white-tailed deer. *Alliaria*'s population growth rate remained explosive where deer had continual access throughout the experiment, but without deer, *Alliaria* is projected to decline to extinction. Our results on the recovery of native species highlight the potential role of biotic resistance and deer-mediated shifts in invader–native community interactions. Upon release from intense deer pressure in the deer exclusion treatment, the three native species exhibited positive fitness responses as measured by their increased reproductive success (Fig. 1*B*). Consequently, *Trillium* exhibited increased seedling recruitment (Fig. 3) and a higher population growth rate where deer were excluded; $\lambda_{per\text{-}year}$ increased from 1.04 with deer to 1.20 in their absence. Indeed, the fitnesses of the native species and *Alliaria* are reversed by changes in the abiotic and biotic contexts in our treatments (Fig. 2 *A* vs. *B*). In addition to suppressing native species as shown here, a companion experiment at our study site (39) demonstrated that deer negatively affect the abiotic context, which could favor short-lived species like *Alliaria* (48). In that study, the area with deer present had significantly more bare ground relative to the area where deer were excluded (39). These openings are likely the combined results of soil disturbances by deer and leaf removal from palatable species in the understory by deer browse, which could increase light levels at the soil surface. Our results point to the restoration of the potent biotic resistance of the native community to *Alliaria* through management of overabundant deer.

Our results also shed light on multiple additional hypotheses for *Alliaria*'s invasion success. Because *Alliaria* cannot flourish in this forest without deer, our results suggest that previous hypotheses for *Alliaria*'s invasion success (48) may be context dependent. In contrast to studies that demonstrate how native herbivores can increase biotic resistance by consuming invaders (18), our findings show that deer, a native generalist ungulate, find the invasive *Alliaria* completely inedible, which undoubtedly bolstered its fitness where deer had access (39, 41). Thus, our data lend support to the hypothesis that a lack of palatability may be a general trait of highly successful invaders (16, 53), particularly in communities with overabundant ungulates (54, 55). Although we did not directly test other hypothesized mechanisms of invasion attributed to widespread exotics including *Alliaria* (i.e., enemy release from specialist herbivores, novel weapons and allelopathy, positive soil feedbacks, competitive ability) (reviewed in ref. 48), our results indicate that either individually or in combination, these mechanisms were not sufficient to maintain *Alliaria*'s population proliferation when

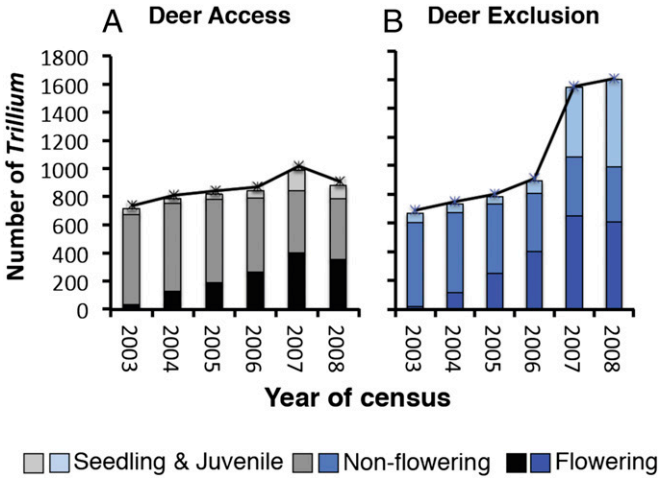

Fig. 3. Total number of the native *Trillium* stems by stage in 2003–2008 pooled across all study plots by treatment: (*A*) deer access and (*B*) deer exclusion. The line shows the trend in total abundance of *Trillium* over the duration of the experiment. Total *Trillium* population size increased dramatically over time in deer exclusion plots, largely due to an increase in seedlings and juveniles. The ratio of flowering to nonflowering adult stems increased more in deer exclusion than deer access plots over time.

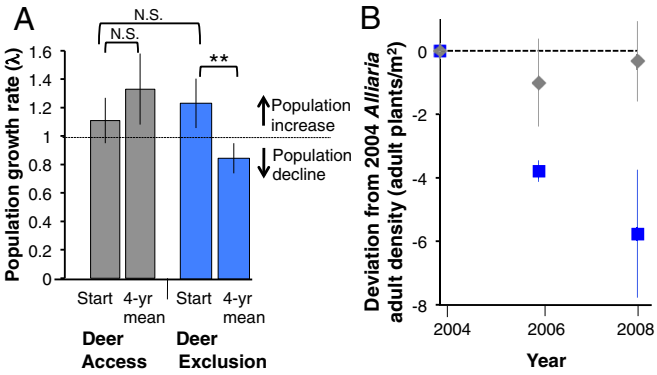

Fig. 4. (*A*) Per year population growth rate ($\lambda \pm$ SEM) of the exotic *Alliaria petiolata* in deer access and deer exclusion plots at the start of the experiment (Start, single transition year 2003–2004) and after 5 y of treatment ($\lambda_{per\text{-}year}$ = time averaged annual growth rate, the fourth root of the 4-y cumulative growth rate). *Alliaria*'s λ declined significantly where deer were excluded, but remained high in deer access plots. (*B*) Deviation of *Alliaria* adult density [adults per square meter (±SEM)] from initial adult density in deer access plots (gray diamonds) and deer exclusion plots (blue squares) 2004–2008. Adult density ranged from 1 to 16 adults per m^2 (mean = 5.4) in deer access plots and from 2 to 17 adults per m^2 (mean = 9.4) in deer exclusion plots. *Alliaria* is a biennial species in which adult plants predominate in alternate years with the rosette-stage plants. Thus, adult densities are shown in 2004, 2006, and 2008 only. *Alliaria* adult densities declined significantly in deer exclusion plots with no change in deer access plots.

deer were excluded. However, these factors may act to further enhance this invader's success in the context of abundant deer.

In forest and rangeland ecosystems across the globe, the domination of native plant communities by exotic species and declines in biodiversity are becoming widespread crises (1, 4, 16). Coincidently, recent changes in management of land, livestock, game, and wildlife have resulted in unprecedented increases in managed (e.g., cattle, goats) and wild native (e.g., deer, moose, elk) ungulate populations worldwide (22, 47, 56). Habitats that experience high ungulate pressure are a recent phenomenon [e.g., overabundant deer and moose in Europe and North America and introduced ungulates in New Zealand and Australia (21–24, 47, 56)] and are likely more susceptible to invasion than those with a long history of browsing (57). If the results of our experiment apply generally, then reducing ungulate numbers where they are overabundant will be key in curbing invasion success in forest and rangelands worldwide. These habitats are in particular need of policy and management practice reform, because their ecosystem functions are predicted to further decline over time as community diversity degenerates (58) and functional redundancy is lost (59). Finally, our findings underscore the need for comanagement strategies for ungulates and invasive plants to maintain functional native–invasive interactions that preserve biodiversity.

Materials and Methods

Field Logistics for All Species. Paired plot locations were chosen in Spring 2002 spanning the range of habitats in this forest where our focal species were found to co-occur. In Fall 2002, we established paired plots (n = 6 pairs of 14 × 14-m plots). One plot per pair was randomly assigned to a fenced treatment that excluded deer, eliminating only deer while allowing all other animals (e.g., turkeys, passerines, rabbits, squirrels, chipmunks, rodents) free access. Fenced plots were enclosed with 3-m-high, 15 × 15-cm steel mesh. Fences were maintained continuously, creating two treatments: deer access and deer exclusion. Each plot contained 36, 4-m^2 subplots, with footpaths every 4 m to ensure minimal disturbance by data collectors. To assess the abundance and the reproductive and browse statuses of *Trillium erectum* (Melanthiaceae), *Maianthemum racemosum* (Ruscaceae), *Polygonatum biflorum* (Ruscaceae), and *Alliaria petiolata* (Brassicaceae) individuals, we determined flowering in early spring, deer browse at time of each species' bloom, and fruiting success in midsummer every year through 2008. Fruiting of the three native species was not assessed in 2003 and 2004; therefore, to approximate the percentage of plants that successfully reproduced (Fig. 1), we assumed that flowering plants that were not eaten or damaged set fruit; otherwise, they did not. Reproduction of natives across treatments and years was compared using G tests. The bite angle of deer is distinct from other mammals, and deer-browsed stems were readily identified.

Matrix Construction for Each Species and Treatment. In our plots, we assessed annual densities (plants per square meter) and measured stage-specific survival and reproduction of the focal species. To calculate the vital rates needed for annual projection matrix construction for *Trillium erectum* and *Alliaria petiolata*, we followed the fates of tagged individuals annually. Details of the field methods and vital rate calculation for each species are presented in *SI Text*. Using the vital rates for *Trillium* (Fig. S2*A*) and *Alliaria* (Fig. S3*A*), we constructed annual population projection matrices, $\mathbf{A}_{\text{YEAR-TREATMENT}}$, with elements a_{ij}, for *Trillium* (Fig. S2*B*) and *Alliaria* (Fig. S3*B*).

For *Trillium*, which varied in abundance among the pairs of plots (and was absent from the habitat represented by one of the pairs), we created a single matrix for each treatment and transition year, pooling data across all plots of a given treatment (fenced vs. unfenced, abbreviated NO_DEER and DEER) for each of the transition years (2003–2004, 2004–2005, 2005–2006, 2006–2007, abbreviated 2003, 2004, 2005, and 2006). This resulted in a site-wide spatial average, where the weighting for *Trillium* was by abundance of individuals in each plot.

For *Alliaria*, which was abundant in all plots, we created separate annual matrices for each plot, six matrices for fenced plots (not accessible to deer) and six matrices for unfenced plots (accessible to deer), for each of the four transition years. Within the range of areas where our focal species were present in Trillium Trail, we chose plots to span the gradient in topography from level to sloped, locating matched pairs along this gradient. We then determined the proportion of the total area of Trillium Trail that was similar to each matched pair. Thus, we were able to apply a weighted average to the data that was representative of the habitats where our focal species were found at the study site. Each plot pair (1–6) was weighted 10%, 10%, 20%, 20%, 20%, and 20%, respectively. To scale up to the level of the entire study site, we created a spatial average by weighting our single plot results accordingly. This resulted in a site-wide spatial average for each transition year and treatment, where the weighting for *Alliaria* was by abundance of the habitat at the site.

For *Trillium*, the transition year 2003–2004 was not considered to measure a pretreatment, baseline condition, because removal of deer (who directly browse this species) has immediate effects on demographic rates. For *Alliaria*, the transition year 2003–2004 was considered to measure a pretreatment, baseline condition, because removal of deer (who alter soil and eat palatable native species) is expected to have a delayed effect on demographic rates. Thus, as a measure of expected population dynamics if deer were maintained at ambient levels, we report the spatially averaged asymptotic population growth rates from the $\mathbf{A}_{\text{2003-NO_DEER}}$ and $\mathbf{A}_{\text{2003-DEER}}$ matrices, $\lambda_{\text{2003-NO_DEER}}$ and $\lambda_{\text{2003-DEER}}$. For this species, our replicates were the plots, and we report the SEs among the plots scaled by the spatial weightings.

In addressing the effects of 4 y of deer exclusion on population dynamics of natives and exotics, we note that population dynamics are multiplicative and effects of deer exclusion are cumulative over time. Thus, we determined multiyear projection matrices **B** for each species and treatment.

For *Trillium* (where we had a single annual projection matrix for each year), $\mathbf{B}_{\text{NO_DEER}} = \mathbf{A}_{\text{2006-NO_DEER}}\,\mathbf{A}_{\text{2005-NO_DEER}}\,\mathbf{A}_{\text{2004-NO_DEER}}\,\mathbf{A}_{\text{2003-NO_DEER}}$, and $\mathbf{B}_{\text{DEER}} = \mathbf{A}_{\text{2006-DEER}}\,\mathbf{A}_{\text{2005-DEER}}\,\mathbf{A}_{\text{2004-DEER}}\,\mathbf{A}_{\text{2003-DEER}}$. We calculated the cumulative population growth rate over a 4-y time step, λ_c (the dominant eigenvalue of each **B**) and its fourth root, $\lambda_{per\text{-}year}$, which measures the time-averaged annual growth rate over the experimental time frame. We constructed 95% bootstrap CIs for each $\lambda_{per\text{-}year}$ to evaluate whether significantly different from 1 (no growth) [n = 5,000 bootstraps (47)]. We used a permutation (randomization) test to evaluate whether $\lambda_{per\text{-}year}$ differed significantly between treatments [n = 5,000 permutations (47)].

For *Alliaria*, we determined **B** for each plot across 4 y and found its dominant eigenvalue and its time-averaged annual growth rate. Then applying the habitat weightings, we calculated a spatially weighted average $\lambda_{per\text{-}year}$ for each treatment at our site. For this species, our replicates were the plots, and we report the SEs among the plots scaled by the spatial weightings.

Multiyear Cumulative Growth Retrospective Analysis. To uncover mechanistic differences between the response of the native and the exotic to deer exclusion, we used a life table response experiment analysis (47), which decomposes treatment-level differences in plant fitness into contributions from each matrix element.

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For *Trillium*, there was one 4-y matrix for each treatment $\mathbf{B}_{\mathrm{DEER}}$ and $\mathbf{B}_{\mathrm{NO_DEER}}$. We defined a reference matrix as the mean across-treatment matrix, used to calculate the sensitivity s_{ij} of λ_c to each matrix element. The difference in matrix elements between treatments is $\Delta b_{ij} = \mathbf{B}_{\mathrm{NO_DEER}} - \mathbf{B}_{\mathrm{DEER}}$. The product ($s_{ij} \times \Delta b_{ij}$) for each element provides its contribution, c_{ij}, to the difference due to the exclusion of deer.

For *Alliaria*, we constructed matrices whose elements were obtained by starting with the 4-y matrices of each plot, **B**. Matrix elements were averaged across plots, weighting each as above for spatial representation of each pair across the study site, to obtain a single *mean*(**B**) and its corresponding λ_c for each experimental treatment. We defined a reference matrix as the mean across-treatment matrix, used to calculate the sensitivity s_{ij} of λ_c to each matrix element. The difference in matrix elements between treatments is $\Delta b_{ij} = mean(\mathbf{B}_{\mathrm{NO_DEER}}) - mean(\mathbf{B}_{\mathrm{DEER}})$. The product ($s_{ij} \times \Delta b_{ij}$) for each element provides its contribution, c_{ij}, to the difference due to the exclusion of deer.

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