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ORIGINAL PAPER

Compounding negative effects of leaf litter absence and belowground competition from an invasive spring ephemeral on native spring ephemeral growth and reproduction

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Abstract Restoring invaded communities requires understanding whether native declines are driven directly by invader competition versus changes to abiotic conditions associated with invader presence. In forest understories, declines in spring ephemerals could result from invasion or by loss of leaf litter layers (associated with invasive earthworms and shrubs) which native ephemerals evolved to emerge from annually. We investigate how native ephemerals (*Erythronium* spp.) are affected by leaf litter absence with and without competition with the functionally similar invader lesser celandine (*Ficaria verna*). The absence of litter reduced *Erythronium* asexual reproduction (corm biomass) by 30%, with reductions magnified to 50% when celandine was also present. Celandine impacts occurred despite celandine having limited aboveground growth under common garden conditions, indicating belowground competition with celandine is sufficient to substantially impact *Erythronium.* This reduced clonal growth would eventually hinder *Erythronium* sexual reproduction because flowering only occurs in large individuals. Both *Erythronium* species responded similarly to treatments: in response to shading from litter, *Erythronium* produced larger and 72–93% heavier petioles and invested less in leaf blade tissue as a proportion of total shoot tissue. Though reduced leaf blade investment was correlated with reduced corm growth, net benefits of litter on growth outweighed negative effects of this biomass allocation tradeoff. These results demonstrate how, although direct competition from invasive plants can impact co-occurring natives, invader-induced changes to local environmental conditions also have important indirect effects. Management supporting native spring ephemerals should prevent losses of or restore depleted forest litter layers as well as reduce invasive competition.

Resumen La restauración de comunidades ecologías que han sido invadidas, requieren saber si la disminución en las plantas nativas resulta por causa de la competencia con plantas invasoras o por los cambios en las condiciones ambientales asociadas con la presencia de las invasoras. En el sotobosque de bosques templados, la disminución en las plantas efímeras de primavera puede resultar de la invasión o de la falta de capas de hojarasca (asociado con lombrices de la tierra y arbustos invasores) con la cual las nativas efímeras han evolucionado para emerger anualmente. Nosotros investigamos como la especie efímera nativa, Erythronium spp., se ve afectada por la ausencia de capas de hojarasca, con y sin competencia con la especie invasora y funcionalmente similar, celidonia menor

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(Ficaria verna). La ausencia de hojarasca redujo la reproducción sexual (biomasa del cormo) de Erythronium en un 30%. Las reducciones aumentaron a un 50% cuando celidonia también estuvo presente. Aunque celidonia tuvo un crecimiento limitado bajo las condiciones de jardín común, su impacto fue evidente. Esto indica que la competencia que ocurre por bajo de la tierra entre Erythronium y celidonia es suficiente para impactar significativamente a Erythronium. La reducción en el crecimiento de Erythronium podría dificultar su reproducción sexual debido a que la ocurrencia de flores solo ocurre en individuos grandes. Ambas especies de Erythronium respondieron de forma similar a nuestros tratamientos: en respuesta a la sombra generada por hojarasca, Erythronium produjo individuos más grandes, 72-93% pecíolos más pesados e invirtieron menos en tejido de la lámina foliar en proporción al tejido total del brote. Aunque esta reducción en inversión estuvo correlacionada con el crecimiento reducido de cormos, los beneficios netos de la hojarasca sobre el crecimiento fueron más importantes que la compensación en la asignación de biomasa. Nuestros resultados demuestran que aunque la competencia directa con plantas invasoras puede impactar las especies nativas cercanas, los cambios en las condiciones ambientales locales que resultan de las invasoras, también pueden tener efectos indirectos importantes. El manejo de especies primaverales efímeras nativas debe tratar de prevenir o restaurar la falta de hojarasca, así como reducir la competencia con especies invasoras.

Keywords Functional traits · Root competition · Invasion impact · Ecological restoration · *Erythronium* · *Ficaria verna*

Introduction

Declines in native understory plant communities have occurred and are predicted to continue due to invasion, herbivore pressure, land use change, and climate change (Augspurger and Buck 2017; Miller and Gorchov 2004; Bialic-Murphy et al. 2020; Lee et al. 2024). When components of the forest understory are replaced by near-monocultures of invasives, above and/or belowground competition from newly dominant species for one or more resources is usually presumed to be the cause. However, alternative drivers, whether associated with invasion or independent from but synchronous with it, can spur native declines while simultaneously creating opportunities for invasive species establishment (MacDougall and Turkington 2005). Restoring such degraded communities requires an accurate understanding of the factors that led to native declines.

Spring ephemerals constitute just 3–4% of all native temperate forest understory herb species (Yancy et al. 2024; Spicer et al. 2020) but are important because they support specialist pollinators (Xie et al. 2025; Bossert et al. 2024; Parker et al. 2016; Wood and Roberts 2018) and reduce nutrient losses at a time of year when vegetation cover is low and leaching and runoff rates are correspondingly high (Chae et al. 2025; Eickmeier and Schussler 1993, Muller and Bormann 1976; but see Rothstein 2000). One potential driver of spring ephemeral decline is the loss of forest litter layers. In deciduous forests of eastern North America, persistent litter has been reduced due to long-term invasion by non-native earthworms (Frelich et al. 2019; Reed et al. 2023) and shrubs, the latter of which commonly have nutrient-rich, quickly decomposing leaves (Arthur et al. 2012; Ashton et al. 2005; Jo et al. 2017). Native spring ephemerals in this region evolved to emerge through litter layers in early spring (Muller 1975, 1978), a strategy with both expected costs and benefits. Litter layers cast shade and are physical barriers to emergence for some species (Sydes and Grime 1981). Yet, leaf litter benefits plants by increasing moisture retention (Donath and Eckstein 2008, Dion et al. 2017) and reducing frost damage by buffering soil temperatures (Sydes and Grime 1981; Baltzinger et al. 2012; Loydi et al. 2014; Tessier 2022). Leaf litter also affects nutrient availability, either directly by increasing supply (Loydi et al. 2014) or indirectly by facilitating fine root growth (Fisk et al. 2004). Overall, we expect net positive effects of litter layer presence, and thus negative effects of its absence, on spring ephemeral growth and survival (e.g., Baltzinger et al. 2012; Dion et al. 2017).

Here, we investigate how two species from a common genus of native spring ephemerals are affected by leaf litter declines, both with and without direct competition with a functionally similar invader. The invader in question, lesser celandine (*Ficaria verna*, syn. *Ranunculus ficaria,* hereafter celandine), occurs in large, dense patches across deciduous forests of

eastern North America (Axtell et al. 2010). Though introduced in 1867, it has only more recently (ca. twenty-first century) colonized large areas and thus raised concerns over a potential ability to competitively exclude natives (Axtell et al. 2010). Like *Erythronium*, celandine is also a spring ephemeral which reproduces both sexually and asexually (Axtell et al. 2010; Mattingly et al. 2023). Celandine readily disperses by washing ashore during river flooding events, and these floodplains range widely in litter depth. Little is known about whether celandine is a driver of leaf litter loss or simply performs well when leaf litter is absent. Leaf litter reduces flowering and seed set in celandine, though biomass does increase with 5 cm of litter relative to none (Masters and Emery 2015b). Some plant species can indirectly affect litter decomposition rates by altering soil physiochemistry and microbial activity, although here also the literature on celandine is sparse. Celandine is more similar to bare soil than it is to the spring ephemerals *Allium ursinum* and *Anemone nemorosa* in its physiochemical effects (Stefanowicz et al. 2023), although its litter decomposition rate, leaf N content and C/N ratios are comparable to that of the ephemerals *A. nemorosa*, *Adoxa moschatellina*, and *Corydalis cava.* These dynamics suggest the effects of celandine on litter decomposition rates may be similar to that of co-occurring native species (Rawlik et al. 2022).

The limited studies that have examined celandine impacts on co-occurring native herbaceous plant performance found mixed results over the short-term. Celandine presence led to decreased biomass of a co-occurring native grass (Masters and Emery 2016) and reduced lifespan and seed set of a native annual forb (Cipollini and Schradin 2011). However, it is associated with increased seed maturation and pollinator visitation rates in co-occurring *Claytonia virginica,* presumably due to higher pollinator activity in invaded plots (Masters and Emery 2015a). As a spring ephemeral, celandine dies back entirely aboveground after late spring senescence, so its impacts may be strongest on co-occurring native spring ephemerals which have a large period of phenological overlap. The magnitude and direction of invader impacts by celandine (or any other invader) on resident native ephemerals will depend on the species and outcome measured, so additional study is needed to examine its full range of ecological effects.

Two species of North American native ephemerals, *Erythronium albidum* and *E. americanum* (Liliaceae), can co-occur with celandine in invaded sites (Masters and Emery 2015a; Oldham 2024; Landsman et al. 2024)). This genus represents 24–30 species of long-lived perennials reproducing primarily asexually through ephemeral subterraneous runners (Fig. 1) that each forms a corm at its terminus (Muller 1978). The parent corm and all runners disintegrate before summer dormancy, with offspring corms persisting (Muller 1978; Fig. 1). Individuals that do not reproduce asexually simply replenish their corm, which then persists. Between senescence in late spring and root renewal in early fall, *Erythronium* remain dormant (Muller 1979, 1975). Though celandine and Erythronium can occur at extremely high densities (several hundred plants per m^2; Masters and Emery 2015a; Axtell et al. 2010; Muller 1975), celandine

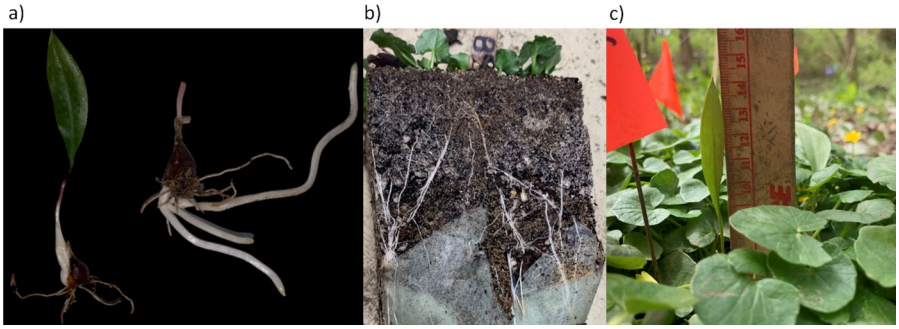

Fig. 1 **a** Morphology of *Erythronium albidum* and *E. americanum*. The petiole runs from the base of the leaf blade to the corm and is pigmented in the portion occurring above the soil surface. Three runners are seen growing from the corm on the right (with shoot removed). **b** The extensive root system of lesser celandine. **c** A naturally occurring *E. albidum* individual with petiole elongated to 10 cm, presumably as a response to the surrounding celandine

biomass per m^2 can be more than an order of magnitude higher than *Erythronium,* (Masters and Emery 2015b; Muller 1975). Celandine's dense growth habit and prolific belowground spread have been hypothesized as mechanisms by which it directly reduces co-occurring native biomass (Masters and Emery 2016; Axtell et al.2010; Kermack and Rauschert 2019). These dynamics suggest belowground competition may influence celandine competitive effect magnitudes. Competition for light likely also occurs, because celandine leaf-out precedes *Erythronium* emergence (Frey and Schmit 2017), reducing soil surface light availability by up to 98% (Authors, unpublished data). However, *Erythronium* light interception is not obviously reduced by celandine because when they co-occur in natural systems *Erythronium* leaf blades often rise above celandine shoots. *Erythronium* leaf blades are supported by a single petiole, which is elongated by up to three times in plants emerging through celandine or leaf litter relative to plants emerging in bare soil (Authors, unpublished data; Fig. 1c). Thus, even if aboveground competition is minimal, *Erythronium* may still incur costs from altering biomass allocation to produce a longer petiole. Petiole growth consumes stored corm resources in the spring before leaf blade development (Muller 1979), and if *Erythronium* invests more resources into petiole elongation when growing amongst celandine, fewer resources may be allocated to leaf blade (*Erythronium*'s main photosynthetic tissue). This tradeoff could ultimately result in fewer resources returned to the corm for future growth and reproduction. Lastly, celandine competition may affect *Erythronium* emergence and flowering phenology, which has performance (growth and reproduction) implications given *Erythronium's* short period of annual aboveground activity. Interspecific competition can induce earlier flowering (Palacio-Lopez et al. 2020), and if similar patterns occur in *Erythronium* then pollinator efficacy and thus its long-term population viability may be impacted.

This study investigates how *Erythronium albidum* and *E. americanum* performance over a full growing season are affected by leaf litter layer absence with and without competition from lesser celandine. We hypothesized that although aboveground interference from celandine and leaf litter may be similar in some ways, the effect of invasive celandine and that of litter loss on *Erythronium* would both be negative. We thus made the following predictions about the performance (growth and reproduction), biomass allocation, and phenology of *Erythronium*:

1. The absence of litter will reduce *Erythronium* performance, which will be further reduced when celandine is also present.
2. Shading from celandine and from litter will cause *Erythronium* to increase petiole and reduce leaf blade investment, which will in turn reduce corm growth.
3. Litter presence and celandine presence will each delay *Erythronium* leaf blade and floral development.

Methods

Plant material

We purchased 189 *Erythronium* corms from commercial suppliers: 89 *E. albidum* (Prairie Moon Nursery, Winona, Minnesota, USA) and 100 *E. americanum* (Tennessee Wholesale Nursery, Altamont, Tennessee, USA). *Erythronium americanum* and *E. albidum* corms arrived on 24 and 27 October 2022, respectively. In November 2022, we harvested actively growing celandine bulbils from a population within deciduous riparian forest in Columbus, Ohio, USA. All plant material was stored for ≤ 3 days at 4 °C before transplanting.

Experimental setup and growth conditions

We planted individual *Erythronium* corms 4 cm below the soil surface depth into 1L pots ($9.2 \times 9.2 \times 15.2$ cm). This depth is common for established *Erythronium* in the field (Muller 1975). Pots contained an equal mixture of coarse sand (Paver Base, Quikrete, Atlanta, Georgia, USA) and propagation mix (LM-AP All Purpose Mix, Lambert, Rivère-Ouelle, Quebec, Canada). We also incorporated slow-release fertilizer pellets according to manufacturer specifications (18 g fertilizer/3.8L soil; Osmocote 14–14–14 Controlled Release Fertilizer, ICL Group, Tel-Aviv, Israel). In November 2022, we buried all but the top 2 cm of each pot into a raised garden bed (7.4×1.3 m) on The Ohio State University campus (Columbus, Ohio, USA). At this time the pot already

contained *Erythronium* and soil described above, and none of these elements were disturbed during burial. To compare light conditions within the garden to those in a nearby forest, we measured photosynthetically active radiation (PAR) at the soil surface on 28 February 2023 using a LI-190R Sensor (LI-COR Biosciences, Lincoln, NE, USA). PAR in the garden was 330 ± 22.9 (mean ± SEM) µmol m^{-2} s^{-1}, in a shady section of the forest was 177 ± 15.0, and in a gap in the forest was 378 ± 19.3. To simulate reduced light availability due to a fully closed forest canopy in mid-spring we covered all pots with a shade cloth 3 m above the soil on 23 April 2023 (light reduction 71.4 ± 2.5%).

Within the garden, each *Erythronium* was stratified into one of six rows based on initial corm biomass such that each row had an equal distribution of similarly sized plants of each species in each randomly assigned treatment (leaf litter, celandine, or bare soil). For the leaf litter treatment (n = 30 *E. albidum* and 33 *E. americanum*), we placed 5 cm of mixed red oak (*Quercus rubra*) and red maple (*Acer rubrum*) leaves on the soil surface (all pots received 7 g of oak leaves by weight, and the maple was split roughly evenly between pots based on visual estimation of volume). Because litter in the main experimental pots was not added based on depth, and because oak litter of the same biomass could vary in volume varied based on the amounts of petioles versus leaf blades (petioles were denser than leaf blades), depths of litter in the pots varied from an estimated 4–7.5 cm. This litter depth in our study design falls between the third quartile and maximum of litter depth measurements taken in a riparian temperate forest in Columbus, Ohio, where both celandine and *Erythronium albidum* co-occurred. This forest contains some invasive shrub cover (*Lonicera maackii*), so we expect our measurements to reflect some leaf litter reduction relative to historical conditions, which we sought to emulate in this study. For the celandine treatment (n = 30 *E. albidum* and 34 *E. americanum*), we planted 5 (± 0.04) grams of recently sprouted celandine bulbils within the top 2 cm of soil. To simulate a forest floor without a litter layer, we grew the remainder (n = 29 *E. albidum* and 33 *E. americanum*) in bare soil. Sample sizes differed slightly due to *Erythronium* availability.

In late December 2022, we realized some of the intended celandine bulbils were misidentified *Viola sororia* rhizomes. We removed all such rhizomes and replaced them with freshly field-collected sprouted celandine on 31 December 2022 and 1 January 2023; across all pots in this treatment, the retained celandine was also removed, weighed, and re-planted to ensure all replicates had a similar amount of disturbance and equivalent celandine biomass (7 ± 0.04 g, an increase over the original 5 g to account for root growth in sprouted celandine bulbils). Because *Erythronium* corms had been planted 2 cm below celandine in each pot (at 4 cm depth), no *Erythronium* was disturbed during this process.

To investigate how our treatments may affect soil temperatures at corm depth we filled twelve 2.9L pots with the soil mix described above and added them to the common garden on 31 December 2022. Each pot was randomly assigned to the three treatments (n = 4 each), buried to the same depth as the main experiment pots. The bare soil was not modified further, the celandine treatment received 7 g of live celandine bulbils planted within the top 2 cm of soil, and the litter treatment received a 7.5 cm deep mixture of red oak and red maple leaves atop the soil surface. Temperature within each pot was recorded by a HOBO MX2201 pendant logger (Onset Computer Corporation, Pocasset, Massachusetts, USA) buried at corm depth (4 cm below the soil surface). Temperature was recorded at hourly intervals between 12 January and 9 May 2023.

Data collection

Growth and reproduction

Immediately before planting, fresh biomass of each *Erythronium* corm was weighed (range 0.20–1.64 g, mean 0.56 ± 0.20 g). Because plants were dormant or had just become active by planting time, these values represent initial belowground biomass.

Within treatments, each *Erythronium* was randomly assigned at planting to one of two harvests: shoot maturity (n = 94) or post-senescence (n = 95). The shoot maturity harvest enabled us to investigate biomass allocation patterns before senescence, when shoot biomass would diminish. Shoot maturity was evidenced by a slight yellowing of the leaf tip (Muller 1978). For this harvest, aboveground dry biomass was the aboveground petiole (hereafter petiole) plus leaf blade, weighed separately. Biomass of the belowground portion of the petiole (from the

soil surface to where the petiole connects to the corm) was excluded from analyses. Belowground dry biomass at shoot maturity consisted of the parent corm plus any runners, weighed separately, but for *Erythronium* grown with celandine, roots could not be separated by species. To estimate the percentage of *Erythronium* belowground biomass that could not be separated, we used *Erythronium* root and runner biomass from the other two treatments. For 58 of 62 *Erythronium* grown in litter or bare soil treatments, roots composed less than 2% of total belowground biomass; the remaining 98% consisted of the parent corm and any runners if present. Thus, we decided not to include root biomass in any treatment for all analysis.

The post-senescence harvest enabled us to determine total corm resource acquisition (or expenditure) during the *Erythronium* growing season. We conducted this harvest between 3 and 8 June 2023, at which point each *Erythronium* shoot had fully senesced, signifying the beginning of summer dormancy. By this point, only dormant offspring corms were alive, and all other plant material (including parent corm, runners, and all aboveground biomass) had senesced. The parent corm transfers its biomass to the dormant offspring corm until the only structures remaining are the husk of the parent corm and the offspring corm, which then become spatially separated, often by a few centimeters (Muller 1979). The fresh weight of each individual corm was recorded. Dry weight was not obtained because these plants were retained for future experiments.

Offspring number at shoot maturity was quantified by counting the number of runners attached to it. If no runners were present, the parent corm was recorded as the only offspring; the *Erythronium* parent corm replaces itself when no runners are present by forming a new corm slightly below the old corm, and then the old corm dies (Muller 1975, 1979). When runners are present, however, reserves from the parent corm are transferred to new corms or runners; in this case, the parent corm becomes depleted and dies at the end of the season (Muller 1979, 1975). Each runner attached to the parent corm therefore indicates future production of an offspring corm. Offspring number at the post-senescence harvest was quantified by counting the total number of corms; at this point all parent corms had died and only offspring corms remained.

Relative growth calculation

Relative growth for each *Erythronium* was calculated as final dry biomass minus initial biomass, divided by initial biomass. Because of phenological differences between the two harvests, final biomass was quantified using different methods. For the shoot maturity harvest, all aboveground and belowground biomass was dried and weighed. For the post-senescence harvest, final dry biomass was estimated from an allometric equation which estimated the relationship between fresh and dry corm biomass based on these measurements taken at the shoot maturity harvest: Log-transformed fresh corm weight reliably predicted log dry corm weight ($R^2 = 0.804$, $n = 73$), so the resulting allometric equation was used to estimate dry corm biomass from fresh:

$$log_{10}(\text{estimated dry biomass}) = (log_{10}(freshbiomass) \times 1.01124) - 0.67210)$$

With this estimate, we could assess relative growth on a dry weight scale. Because initial biomass could only be weighed fresh, we estimated dry initial biomass using the equation above. Hereafter, *initial biomass* refers to these estimated dry biomass values. In all cases, relative growth < 0 signifies a net biomass loss. To ensure our inferences were robust to how relative growth was estimated, we also calculated relative growth using log response ratios. Results did not differ, so we present only the former analysis here.

Biomass allocation

At the shoot maturity harvest, leaf blade and petiole lengths and widths were measured to estimate leaf area and petiole volume and then dried at 60 °C and weighed. Petiole samples were lost for 23 individuals, so for these samples petiole biomass could not be weighed and they were dropped from biomass allocation analyses. We approximated leaf blade area as the area of an ellipse ($0.5 \times$ leaf blade width $\times 0.5 \times$ leaf blade length $\times \pi$) and petiole volume as the volume of a right cylinder ($((0.5 \times \text{petiole width})^2 \times \pi \times$ petiole length). To investigate how treatments affected tissue construction, we calculated specific leaf blade area (g/cm^2) and petiole biomass per unit volume. A

lower petiole biomass per unit volume would signify etiolation or similarly investing in a lower density of tissue, potentially enabling *Erythronium* to escape aboveground cover by gaining height with presumably 'cheaper' tissues. The spring ephemeral *Claytonia virginica* reduced leaf biomass per unit volume in response to shading (Eickmeier and Schussler 1993), and *Sphagnum* reduced stem mass per unit length in shading (Norby et al. 2023), so we expect a similar response from *Erythronium*. We quantified investment in leaf blade tissue as a proportion of total aboveground biomass (leaf blade biomass divided by total shoot biomass [leaf blade + petiole]). We expected this measure, which we refer to as *leaf blade investment*, would decline with increased relative allocation to petiole biomass. Lastly, we quantified belowground biomass allocation as root mass ratio (belowground biomass divided by total biomass).

Phenology

Erythronium shoot development was monitored between the first emergence (3 January 2023) and shoot maturity (6 April 2023). Plants were monitored weekly between January 3 and March 18, except for one week in February (measurements taken on February 16 and March 2). In late March, phenology began to progress quickly, so plants were monitored at 3-day intervals between March 18 and March 27. The final phenological monitoring timepoint was April 6. For each individual, the dates of shoot emergence, leaf maturation, flower emergence, and petal opening were recorded. Shoot emergence was defined as the first date upon which the shoot had emerged from cover (i.e., litter, celandine, or soil). Leaf maturation occurred when the leaf was fully expanded as denoted by a convex shape of the blade (Muller 1978, 1979) accompanied by advanced development of chlorophyll (leaves visibly changed color from mottled brown and green to solid bright green). Flower emergence occurred when any part of the inflorescence was visible (usually the emergence of the peduncle). When the individual petals of the inflorescence were distinguishable, petal opening was recorded. A few of the flowering individuals produced fruit, but fruiting data was not recorded because it occurred after the data collection period for phenology (we did not measure plants through senescence).

From these dates, we derived four phenological responses of interest. *Shoot emergence* was recorded as the day of year that event occurred. *Days to flower emergence* was the number of days between shoot emergence and flower emergence, and *petal opening period* was the number of days between flower emergence and petal opening. Similarly, *leaf maturation period* was the number of days between shoot emergence and leaf maturation.

We assessed the timing of celandine aboveground growth and thus its potential to influence abiotic conditions and *Erythronium* growth or phenology. Absolute cover of celandine shoots and absolute cover of celandine shoots at or above the height of *Erythronium* were visually estimated at 7–10 day intervals between 17 January and 6 April 2023. Each *Erythronium* and any surrounding celandine were measured on every sampling date. Celandine was the only vegetation in the pot other than *Erythronium*, and the only *Erythronium* biomass at the soil surface was its petiole base (< 1 mm diameter).

Statistical analysis All analyses were executed using R version 4.2.2 (R Core Team 2022). We calculated inferential statistics using type II sums of squares in the package "car" (Fox and Weisberg 2019), incorporated random effects as needed using "lme4" (Bates et al. 2015), and conducted post-hoc pairwise comparisons using "emmeans" with false discovery rate (FDR) adjustments (Lenth 2023). Unless otherwise indicated, we present estimates of variability as standard error of the mean.

For each temperature logger, the range, minimum, and maximum temperatures were calculated for each day of deployment. These daily temperature metrics were included in linear models with planting treatment as a main effect and day and logger as random effects.

Relative growth, offspring number and biomass, all biomass allocation metrics, and all phenology metrics were compared among treatments using linear models with treatment, species, and the treatment × species interaction as fixed factors and initial biomass as a covariate to account for variation in starting corm size. To investigate if relative growth was moderated by leaf investment, we fitted a linear model with leaf investment, treatment, species, the treatment × species interaction, and initial biomass as predictors.

We also assessed the probability of flowering as a function of these predictors using binomial regression with a logit link function. Because only one *E. americanum* in the bare soil treatment had a recorded petal opening, the treatment × species interaction effect on petal opening could not be included in the model for petal opening period. Offspring weight distributions were compared across treatments using two-sample Kolmogorov–Smirnov tests. All these analyses were run separately by harvest.

Results

The vast majority (94%, 177 of 189) of our planted *Erythronium* survived. *Erythronium americanum* and *E. albidum* responded similarly to all treatments ($P > 0.12$ for the effect of species and interactions with species across all analyses), so for simplicity we omit mention of these similarities for the remainder of the Results (see Supplemental Information for figures showing species-specific responses).

Treatment effectiveness

Leaf litter presence affected temperature fluctuations, buffering daily temperature range (Fig. S1a) and maxima (Fig. S1b; $P < 0.01$ for both responses), although treatments did not affect daily minima (Fig. S1c; $P = 0.14$) nor averages (Fig. S1d; $P = 0.79$). Daily temperature ranges between bare soil and celandine treatments did not differ but were > 50% greater in magnitude than temperature ranges in litter (in bare soil, 6.09 ± 0.18 °C; in celandine, 6.26 ± 0.19 °C; and in litter, 3.94 ± 0.12 °C; $P < 0.01$; Fig. S1a). Daily maxima, similarly, did not differ between bare soil and celandine treatments but were 12–15% higher than those in litter (bare soil, 11.9 ± 0.34 °C; celandine, 12.1 ± 0.35 °C; and litter, 10.5 ± 0.29 °C; FDR $P < 0.01$; Fig. S1b).

By the end of *Erythronium*'s active growth phase, celandine growth aboveground was less developed than in nearby field populations, presumably due to our relatively late re-planting date. Mean celandine cover at the time of *Erythronium* emergence was 38.8 ± 0.69%, whereas celandine cover at or above the height of *Erythronium* was just 11.3 ± 0.36%. This likely resulted in weaker aboveground interactions between celandine and *Erythronium* relative to field conditions.

Growth and asexual reproduction

Erythronium growth in litter and bare soil was always greater than when grown with celandine, though differences between litter and bare soil treatments depended on *Erythronium*'s developmental stage (Fig. 2; Table 1). At shoot maturity, *Erythronium* in litter and bare soil had on average nearly tripled in biomass relative to initial biomass

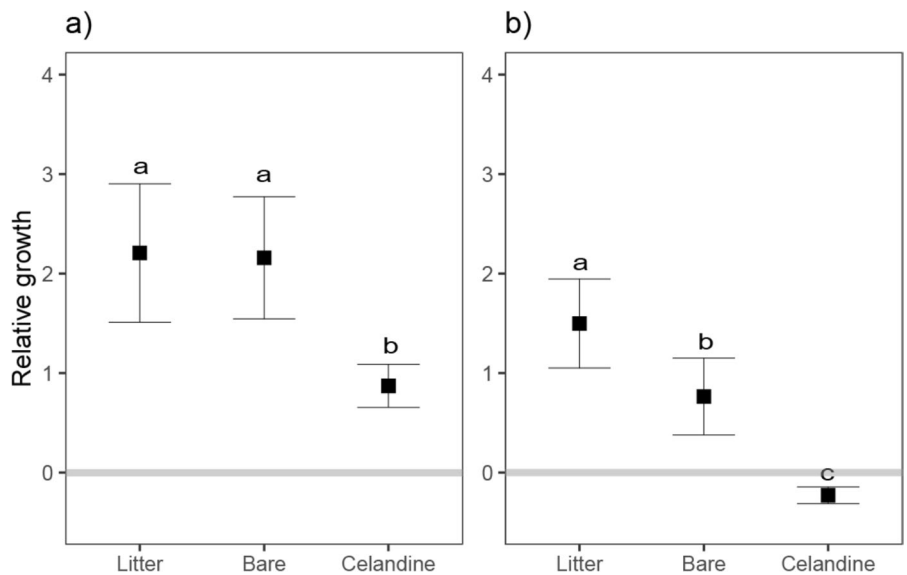

Fig. 2 Relative growth of *Erythronium* when grown under a cover of leaf litter, in bare soil, or with lesser celandine (where litter was also absent). Growth was recorded **a** at shoot maturity and **b** after senescence. Error bars represent 95% CI. The grey lines at 0 indicate final biomass equal to initial biomass. Letters represent significant pairwise differences within a given panel

Table 1 Effects of treatment, species, and initial biomass on *Erythronium* growth and reproduction

Trait	Predictor	F-statistic	*P*
Relative growth (harvest at shoot maturity; n = 56)	**Treatment**	**6.67**	**< 0.001**
	Species	2.54	0.117
	Treatment x species	1.47	0.239
	Initial biomass	**12.52**	**< 0.001**
Relative growth (harvest post-senescence; n = 84)	**Treatment**	**28.45**	**< 0.001**
	Species	0.00	0.976
	Treatment x species	0.37	0.694
	Initial biomass	**21.87**	**< .001**
Offspring number (harvest at shoot maturity; n = 83)	Treatment	0.05	0.951
	Species	0.68	0.412
	Treatment x species	0.35	0.704
	Initial biomass	0.97	0.329
Offspring number (harvest post-senescence; n = 87)	Treatment	1.24	0.294
	Species	0.03	0.861
	Treatment x species	0.60	0.553
	Initial biomass	0.45	0.507
Total offspring biomass (g) (harvest post-senescence; n = 84)	**Treatment**	**30.62**	**< 0.001**
	Species	0.04	0.835
	Treatment x species	0.21	0.811
	Initial biomass	2.32	0.131

Bolded results are significant at $P < 0.05$

(litter treatment final 0.339 ± 0.033 g versus initial 0.127 ± 0.011 g; bare soil final 0.302 ± 0.025 versus initial 0.115 ± 0.010 g), an increase that did not differ between them (FDR $P = 0.830$) but was greater than when grown with celandine (final 0.208 ± 0.018 g versus 0.113 ± 0.011 g initial; Fig. 2a). Post-senescence, however, relative growth in litter was nearly twice as high as in bare soil (FDR $P < 0.01$; Fig. 2b; Table 1), and *Erythronium* in celandine had experienced a net loss of corm biomass (Fig. 2b).

Reproductive output when measured as offspring number was not affected by treatment at either harvest (Table 1). However, *Erythronium* total offspring biomass was more than halved by celandine presence and decreased by 30% in the absence of litter (litter treatment 1.170 ± 0.087; bare 0.821 ± 0.069; celandine 0.456 ± 0.045 g; FDR $P < 0.001$ for both comparisons; Table 1). Per-corm biomass post-senescence was also affected, as illustrated by comparing distributions of individual offspring corm weights (Fig. 3). Nearly every *Erythronium* offspring corm was small (< 0.05 g) when parent plants were

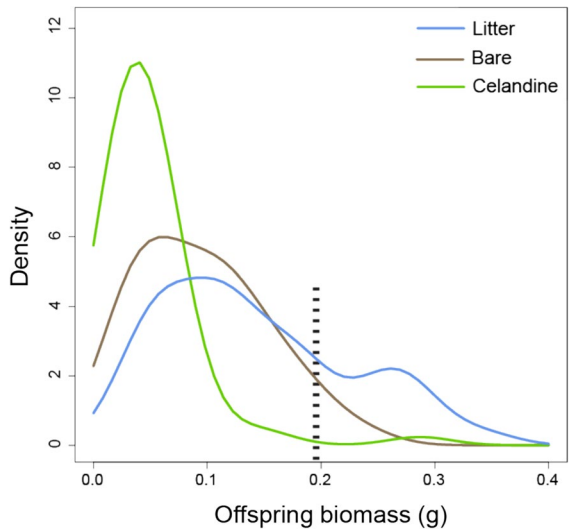

Fig. 3 Density plot of individual offspring biomass for *Erythronium* under the three planting treatments. Dashed line indicates the putative biomass threshold required for *Erythronium* flowering (0.196 g), based on flowering incidence from corms with known biomass in the preceding growing season

grown with celandine, whereas the other two treatments enabled the production of larger corms (Kolmogorov–Smirnov $P < 0.001$ for both pairwise comparisons). These distributions were similar for plants growing in bare soil or with litter ($P = 0.092$).

Biomass allocation

Erythronium in litter had on average 72–93% heavier petioles than when growing in either celandine or bare soil (Fig. 4a), with similar petiole biomass in the latter two treatments (FDR $P = 0.864$; Table 2), and similar leaf blade biomass across treatments (Fig. 4b). In contrast, petiole biomass per unit volume trended higher in celandine than in bare soil (FDR $P = 0.074$; overall treatment effect $P = 0.034$), though it did not differ between litter and any other treatment (Fig. 4c). Neither specific leaf area nor root mass ratio differed among treatments (Fig. 4d, f; Table 2). The increase in *Erythronium* petiole biomass when grown in litter, coupled with a lack of treatment effects on leaf biomass, also meant that leaf blade investment (blade biomass as a proportion of total shoot biomass) was lower in leaf litter than in bare soil (FDR $P < 0.05$) and trended lower than in celandine (9.3% and 6.9% reductions relative to bare soil and celandine, respectively; Fig. 4e; Table 2).

Increased leaf blade investment was associated with greater corm growth, as expected, although this relationship was marginally significant ($\beta = 4.280$; $P = 0.064$; model $R^2 = 0.408$; treatment and initial biomass main effects both $P < 0.01$; Fig. 5). We found no support for this relationship varying by treatment.

Phenology and flowering

Leaf litter absence hastened *Erythronium* shoot emergence by 14–16 days relative to other treatments but prolonged subsequent leaf maturation by the same duration (Table 3; Fig. 6a, b). A one standard deviation (0.059 g) increase in initial biomass was associated with a 16-day earlier shoot emergence but a 5-day longer leaf maturation period ($\beta = -275.93$ and 83.17, respectively; $P < 0.0001$; Fig. 6a, b).

Days to flower emergence was hastened by 14–15 days when litter was absent (a marginally significant effect; Table 3, Fig. S2a). Petal opening period was also prolonged by 14–16 days when litter was absent relative to both other treatments (marginally significant; Table 3, Fig. S2b). Flowering phenology was unrelated to initial biomass (Fig. S2c, S2d). Of the 179 surviving *Erythronium*, only 12% flowered. *Erythronium* with larger initial biomass were more likely to flower ($P < 0.001$), but flowering was unaffected by treatment or species identity (all $P > 0.14$). With only one exception, all flowering *Erythronium* had an initial biomass ≥ 0.196 g (Fig. 3; Fig. S2c). Of all offspring corms produced by the end of our experiment, 34% of those whose parental corm was grown in litter grew to be larger than this putative biomass threshold, whereas only 9% of corms in bare soil and 2% (one individual) in celandine did (Fig. 3), suggesting sexual reproduction the following year would be much more likely where litter occurred and almost nonexistent where litter was absent and celandine present.

Discussion

We document clear reductions in *Erythronium* performance by leaf litter absence alone, a treatment designed to simulate long-term forest invasion from earthworms and non-native shrubs with rapidly decomposing leaves. These performance declines were even greater when litter absence was coupled with direct competition from celandine. Thus, impacts of invader-induced changes to local abiotic conditions can be compounded when direct invader competition is also present—in this case, with implications for sexual reproduction and thus long-term population viability. These results highlight the importance of a dual management strategy, ideally reducing celandine while also restoring leaf litter in forests where spring ephemerals occur.

Leaf litter absence reduced native performance independently of invader competition

Our finding that leaf litter presence greatly benefitted *Erythronium* reflects the effects of litter alone, independent from factors that are often confounded with litter dynamics in field studies (e.g., earthworm presence and the composition of neighboring plant communities; Wood and Bornstein 2011). These are likely underestimates of the true benefits to *Erythronium* under field conditions, where larger expanses of litter should cause greater effects than documented

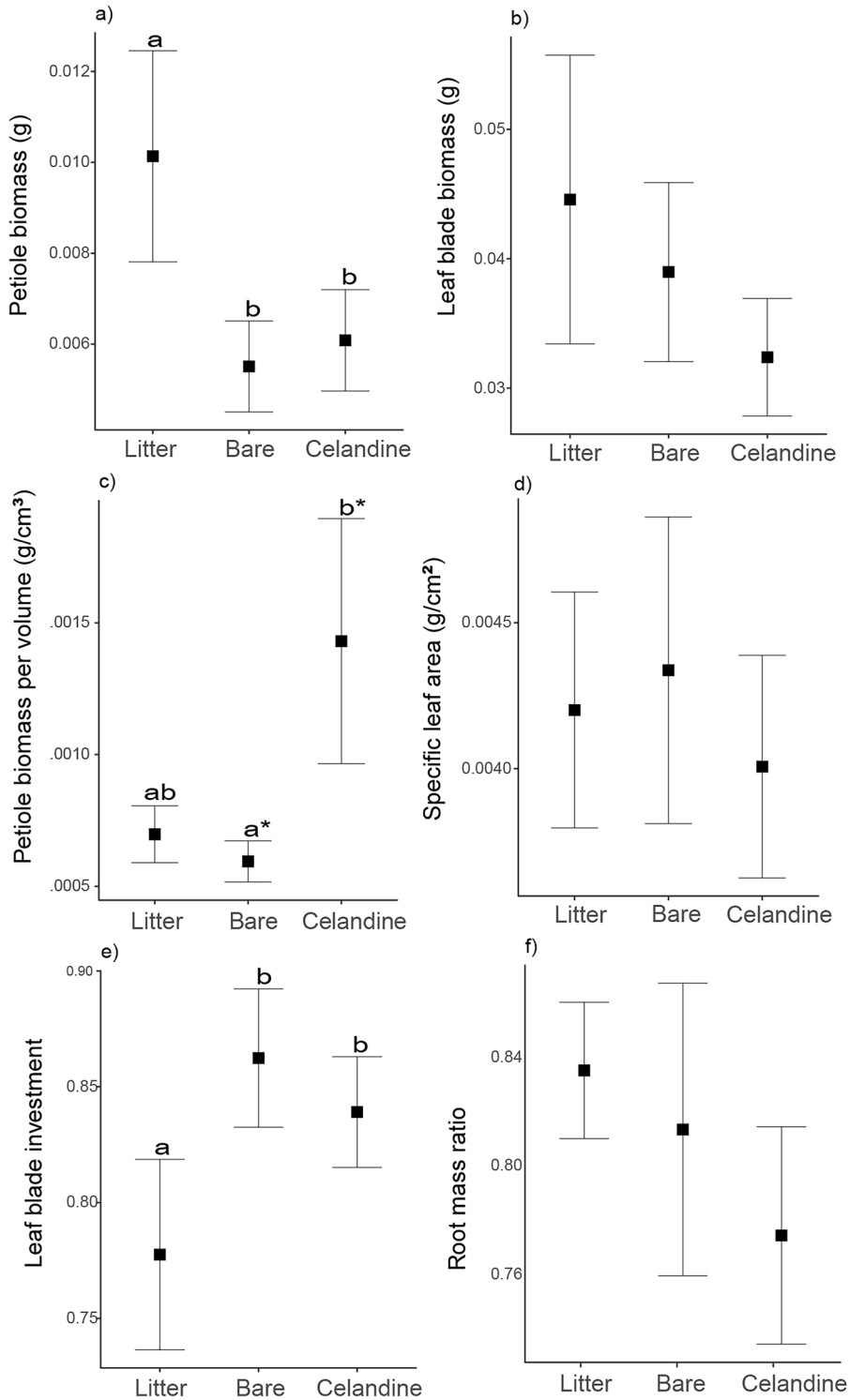

Fig. 4 *Erythronium* biomass allocation patterns when grown under the three planting treatments, including **a** petiole biomass, **b** leaf blade biomass, **c** petiole biomass per volume, **d** specific leaf area, **e** leaf blade investment and **f** root mass ratio. Error bars represent 95% CI. Letters represent significant pairwise differences within a given panel. Note that in panel **c** the pairwise difference between bare soil and celandine was marginally significant ($P = .074$)

Table 2 Effects of treatment, species, and initial biomass on *Erythronium* biomass allocation, based on harvest at shoot maturity

Trait	Predictor	F-statistic	*P*
Petiole biomass (g) (n = 66)	**Treatment**	**7.44**	**0.001**
	Species	0.71	0.404
	Treatment x species	0.01	0.990
	Initial biomass	0.32	0.576
Leaf blade biomass (n = 68)	Treatment	1.74	0.183
	Species	0.70	0.408
	Treatment x species	0.09	0.915
	Initial biomass	0.23	0.635
Petiole biomass per volume (g/cm^3) (n = 33)	**Treatment**	**3.87**	**0.034**
	Species	1.69	0.204
	Treatment x species	.427	0.657
	Initial biomass	.071	0.792
Specific leaf area (g/cm^2) (n = 62)	Treatment	0.36	0.698
	Species	1.10	0.299
	Treatment x species	0.76	0.475
	Initial biomass	0.09	0.769
Root mass ratio (n = 56)	Treatment	0.92	0.407
	Species	1.91	0.174
	Treatment x species	0.36	0.700
	Initial biomass	1.07	0.305
Leaf blade investment (leaf blade biomass: total shoot biomass; n = 62)	**Treatment**	**4.07**	**0.023**
	Species	0.23	0.630
	Treatment x species	0.09	0.919
	Initial biomass	0.02	0.883

Bolded results are significant at $P < 0.05$

in pot experiments. Also, our relatively short-term experiment using litter composed of just two tree species may not have fully captured effects of microbial activity associated with leaf litter. Though microbial effects can develop within months (Habtewold et al. 2020), those in uninvaded or newly restored forests develop over decades (Sun and Badgley 2019; Banning et al. 2011; Sun et al. 2017). We included red oak and red maple litter due to the dominance of these species in riparian forests and to get a blend of fast and slow-decomposing litter (red oak has relatively persistent litter whereas red maple decomposes faster). Because many other tree species occur in northern temperate forests, and litter properties vary greatly across tree species (Simon et al. 2018; Wu et al. 2013), we encourage future research investigating species-specific litter effects on spring ephemerals.

The mechanisms by which leaf litter affected conditions in our experiment included reductions in diurnal temperature maxima and fluctuations (Fig. S1), adding to a growing body of evidence for its temperature buffering effects (Sydes and Grime 1981; Donath and Eckstein 2008; Loydi et al. 2014; Dion et al. 2017). Litter presence also increases moisture retention (Donath and Eckstein 2008), and reduced temperature maxima could contribute to reduced moisture losses from evapotranspiration. Where leaf litter remains, such effects could lessen the impact on understory flora of late-spring heatwaves, which are increasing in frequency and intensity due to climate change (Calvin et al. 2023). The temperature buffering magnitude experienced by our experimental *Erythronium* was likely not as high as that recorded in the temperature monitoring pots with litter because the litter depth in these pots varied. Yet, the temperature dynamics and the changes in *Erythronium* phenology we observed under litter show strikingly similar patterns (Figs. 6, S1, S2), strongly suggesting that delayed *Erythronium* shoot emergence and initiation of flower development in the presence of litter

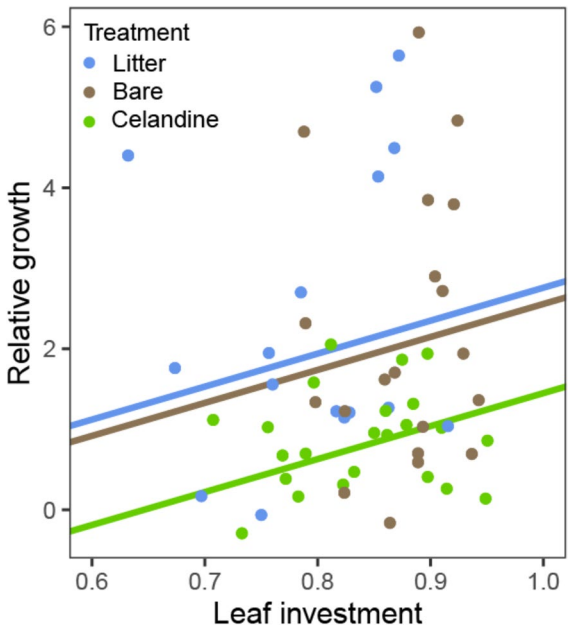

Fig. 5 *Erythronium* relative growth as a function of leaf blade investment, plotted separately for each planting treatment. Regression lines reflect parameter estimates from the best-fit model

resulted from litter-induced buffering of temperature fluctuations.

The implications of these phenological shifts for *Erythronium* were apparently negligible in our study, because delays in leaf or flower initiation were coupled with shorter maturation periods such that plants reached maturity at the same time across treatments. Delays in emergence could be beneficial to *Erythronium*; frost damage causes earlier senescence in this genus (Tessier 2022), so if later emergence reduces exposure to frost damage, this delayed phenology could potentially be adaptive. These predictions become more complicated when considering impacts of climate warming, which has hastened emergence timing in *Erythronium americanum* (Tessier 2019) as well as many woody plants (Dawson-Glass et al. 2025). Similarly, interannual temperature increases have been associated with earlier seasonal emergence in the herbaceous perennials *Poa annua* (March-Salas and Pertierra 2020) and *Gunnera tinctoria* (Mantoani et al. 2020), but also hastened the dates of last frost, leading to uncertainty as to whether phenological shifts will impact frost risk for a given species (Park et al. 2021). Ultimately these dynamics will be system-specific and warrant further investigation in ecosystems with spring ephemerals.

Positive effects of leaf litter in our study occurred *despite* inducing biomass allocation shifts that could negatively affect *Erythronium* growth and reproduction. Similar to classic etiolation as a shade-avoidance response (Darwin and Darwin 1880), our *Erythronium* responded to litter cover by elongating petioles. Contrary to expectations based on other species (Eickmeier and Schussler 1993; Norby et al. 2023), the *Erythronium* response to shading

Table 3 Effects of treatment, species, and initial biomass on *Erythronium* phenology

Event	Predictor	F-statistic	*P*
Shoot emergence date (n = 178)	**Treatment**	**8.67**	**<.001**
	Species	0.61	.436
	Treatment x species	0.46	.633
	Initial biomass	**92.60**	**<.001**
Leaf maturation period (n = 176)	**Treatment**	**43.96**	**<.001**
	Species	1.86	.175
	Treatment x species	0.02	.983
	Initial biomass	**45.73**	**<.001**
Days to flower emergence (n = 20)	*Treatment*	*3.38*	*.066*
	Species	0.00	.974
	Treatment x species	0.934	.418
	Initial biomass	0.08	.780
Petal opening period (n = 18)	*Treatment*	*2.93*	*.096*
	Species	0.42	.531
	Initial biomass	0.08	.781

Bolded results are significant at $P < 0.05$, and italicized results are marginally significant at $0.05 < P < 0.10$

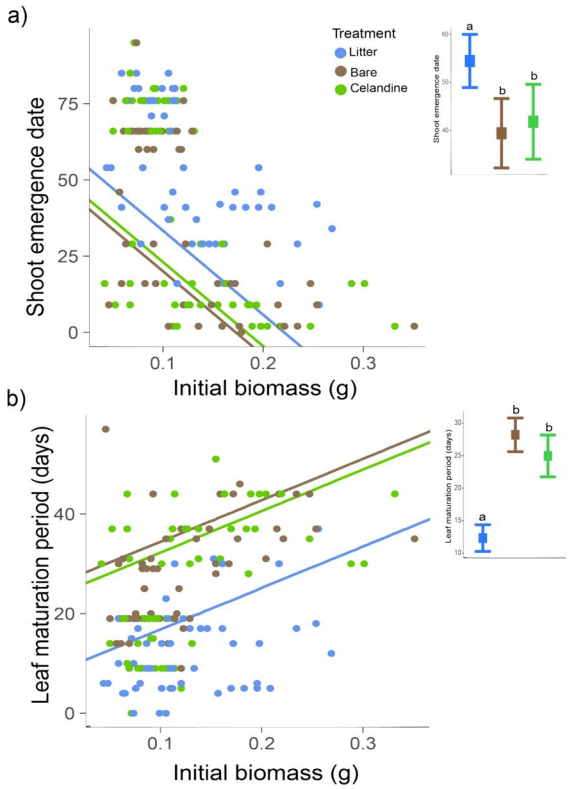

Fig. 6 *Erythronium* phenology variation under the three planting treatments and as a function of initial biomass, including **a** shoot emergence date and **b** leaf maturation period. Results presented in the inset figures are treatment means and 95% CI, with letters indicating significant pairwise differences between treatments

from leaf litter did not lead to reduced petiole biomass per unit volume. Instead, our *Erythronium* apparently allocated biomass into petiole tissue that would otherwise have been allocated to leaf blade. Either response could be costly by reducing relative investment in photosynthetic tissue, leading to fitness reductions in the presence of litter as observed in the spring ephemeral *Obolaria virginica* (Wood and Bornstein 2011). Yet, despite leaf blade investment being positively associated with relative growth across treatments (Fig. 5), and despite leaf blade investment being lowest in the presence of leaf litter (Fig. 4e), *Erythronium* in our study grew more in the presence of leaf litter (Fig. 2b). Therefore, the negative effects of shoot elongation are more than offset by the benefits associated with leaf litter. Similar patterns occur in the spring ephemeral *Anemone nemorosa*, which elongates petioles under leaf litter with no net negative effects on rhizome growth (Baltzinger et al. 2012).

Direct belowground competition with invader reduces native growth and fecundity

Existing studies have found reduced fecundity in natives grown amongst celandine (Cipollini and Schradin 2011; Masters and Emery 2015a). We show that celandine also reduces corm growth and asexual reproduction in long-lived natives. Though celandine presence did not impact *Erythronium* offspring number, celandine did reduce *Erythronium* total asexual reproductive biomass. (Figs. 2b and 3). Belowground competition was probably the major driver of these declines because by *Erythronium* shoot maturation, celandine roots occupied most of the belowground pot volume, despite leafing out several weeks after *Erythronium* emergence and never growing large enough to shade it. Also, aboveground biomass of celandine at harvest was not correlated with any metric of *Erythronium* performance (data not shown). The negative effects of celandine on *Erythronium* reported here are thus conservative estimates of its impact in the field. In the field, belowground competition is likely to be even more pronounced because of accumulated celandine root biomass. Aboveground competition would also be expected because celandine leaf-out precedes that of *Erythronium* by several weeks, leading to crowding aboveground. Our results highlight the importance of documenting belowground competition effects, which for herbaceous species are generally greater than aboveground competition (reviewed by Kiær et al 2013).

Erythronium flowering likelihoods were greater in plants that began the growing season as larger corms, consistent with prior observations (Muller 1979). Celandine-induced reductions in *Erythronium* offspring would thus presumably reduce future flowering of the offspring (see Fig. 3). In combination with widespread leaf litter losses, our results suggest that celandine invasions reduce *Erythronium* flowering likelihoods to nearly zero. This has clear implications for the long-term population viability of *Erythronium* and the specialist pollinators they support. Although these inferences do contrast with a lack of treatment effects on flowering probability reported above, we

attribute this latter result to the fact that flowering during our experiment was influenced primarily by initial corm biomass (before treatments began), rather than by growth during the experiment.

Though *Erythronium* survival across treatments was high in our one-year experiment, this duration may have been insufficient to detect declines in such long-lived perennials. Miller and Gorchov (2004) made a similar argument about the potential negative effects of invasive *Lonicera maackii* on native forest herbs, despite detecting no direct effects on survival. Longer-term experiments and demographic studies (e.g., Bialic-Murphy et al. 2020) are needed to substantiate or refute inferences about invasion impacts from shorter-term experiments.

No functional differences between *E. albidum* and *E. americanum*

Many *Erythronium* species are locally abundant and ecologically important throughout their native ranges (Austen et al. 2018; Muller and Bormann 1976; USDA 2014; Pupillo and Astuti 2017), yet studies examining interspecific differences are lacking. Though our species' ranges largely overlap in Eastern North American forests, only *E. americanum* extends into the extreme southeast and northeast, and *E. albidum* alone extends west into the prairie states (USDA 2014). We found no significant differences between these species in biomass allocation, reproduction, nor response to invaders. However, because *E. albidum* occurs in areas of higher soil moisture relative to *E. americanum* (Prince 2008), we expect that negative population-level implications due to celandine invasions, which predominate in floodplain habitats, will be greater across the range of *E. albidum* than *E. americanum*. Given their importance for ecosystem functioning and maintaining biodiversity of both plants and specialist pollinators, it is critical to understand how responses to changing conditions vary between spring ephemeral species.

Conclusions

Based on the results presented here, and the widespread occurrence of litter reductions and invasive celandine across our region, we would expect to see continued population declines in these *Erythronium* species. This suggests management of celandine is warranted, despite reports that celandine presence can increase seed set in nearby *Claytonia virginica* (Masters and Emery 2015a). We also encourage further research investigating how celandine affects pollinator populations in its invasive range. We speculate that negative impacts from celandine and other invasives may be especially underestimated in spring ephemeral communities due to the combination of their short period of annual aboveground activity and tendency towards long-lived perennialism that may yield subtle changes over short timeframes. Our results also highlight the importance of litter layer preservation, for example by replacing invaders that have quickly decomposing leaves with natives that produce more recalcitrant leaf litter. Deep litter layers (~ 20 cm) are also detrimental to celandine reproduction (Masters and Emery 2015b), which could additionally help by introducing feedbacks that reduce its competitiveness against native ephemerals.

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Author contributions GRG and SMH conceived the ideas and designed methodology. GRG collected the data; both authors analyzed the data; GRG led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication. All intellectual contributions and other work associated with this study were undertaken in the home country of both authors.

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Data availability All data, code, and software necessary to re-create the analyses and figures presented in this text are publicly available through DRYAD via this DOI: https://doi.org/10.5061/dryad.t76hdr8b1.

Declarations

Competing interests The authors declare no competing interests.

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