

Invasion-induced root-fungal disruptions alter plant water and nitrogen economies.

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Abstract

Despite widespread evidence that biological invasion influences both the biotic and abiotic soil environments, the extent to which these two pathways underpin the effects of invasion on plant traits and performance is unknown. Leveraging a long-term (14-yr) field experiment, we show that an allelochemical-producing invader affects plants through biotic mechanisms, altering the soil fungal community composition, with no apparent shifts in soil nutrient availability. Changes in belowground fungal communities result in high costs of nutrient uptake for native perennials and a shift in functional traits linked to their water and nutrient use efficiencies. Some species in the invaded community compensate for high nutrient costs by reducing nutrient uptake and maintaining photosynthesis by expending more water, which demonstrates a trade-off in trait investment. For the first time, we show that the disruption of belowground nutritional symbionts can drive native plants toward novel regions in order to maintain their water and nutrient economics.

Main text

Invasive plants have strong negative impacts on population dynamics of native species, community assemblages, and ecosystem processes (Wilcove *et al.* 1998). Two hypotheses may explain the impacts of invasive species on native ecosystems: (1) shifts in soil resource availability (Davis *et al.* 2000; Ehrenfeld *et al.* 2001) and (2) disruption of belowground microbial-mediated resource provisioning (Traveset & Richardson 2014). Both pathways result in the same physiological signature of resource limitation for native plants and are therefore difficult to disentangle with physiological trait measurements alone. Moreover, while evidence supports both invasion hypotheses individually, invasive species commonly modify abiotic soil

resources and disrupt biotic interactions simultaneously and the cascading effects of invasion belowground are rarely linked to aboveground impacts (Blumenthal 2006; Zhang *et al.* 2019). Gaining new insight into the mechanisms underlying successful plant invasion requires tracing invasion-induced changes in belowground soil dynamics to shifts in native plant traits and performance.

Many invasive species increase the quantity and quality of leaf litter and rhizodeposition, leaving long-lasting effects on abiotic soil resource availability and carbon, nitrogen, and water cycles (Ehrenfeld *et al.* 2001; Allison & Vitousek 2004). If invasive species increase nutrient concentrations, belowground microbial mutualisms with native species may be disrupted (Figure 1c) (Johnson 2010). Other invasive species may have specialized roots or high root density, making the invasive species superior to natives at capturing limited resources (Funk 2013). If invaders are superior soil resource competitors, invasive species will deplete soil resource availability to lower levels than can be tolerated by native species (Tilman 1982), resulting in physiological stress and reduced native plant performance (Figure 1b).

While only recently investigated as a mechanism of invasion success, many of the world's most successful invaders alter soil microbiome abundance and diversity and disrupt plant-microbial interactions (Reinhart & Callaway 2006; Dawson & Schrama 2016). Invasion-induced changes in soil microbiomes are driven by specialized microbial associations with non-native plant hosts (Husband *et al.* 2002; Vandenkoornhuyse *et al.* 2002), altered plant diversity (Kivlin & Hawkes 2011), altered plant-soil feedbacks (van der Putten 2010), and direct toxicity of soil microbes via the production of allelochemicals (Hierro & Callaway 2003). A shift in soil microbiome

abundance and diversity and the disruption of plant-microbial interactions can have dramatic effects on soil resource provisioning to native plant partners (Wang *et al.* 2017). Among the most important plant-microbial symbionts for resource exchange is the association between arbuscular mycorrhizal (AM) fungi (Glomeromycotina) that obligately live in plant roots of at least 70% of land plant species (Soudzilovskaia *et al.* 2020). The foundation of this symbiosis is a two-way exchange of resources: AM fungi receive 20-40% of their host plant's carbon (C) (Drigo *et al.* 2010), and in turn boost the supply of soil resources (water, phosphorus (P), and nitrogen (N)) to their host plant (Smith *et al.* 2003; Parniske 2008; Yang *et al.* 2012). If the mechanism driving reduced native plant performance following biological invasion is the disruption of soil resource provisioning by microbial symbionts (mutualism disruption hypothesis (Hale & Kalisz 2012)), then biological invasion would induce physiological stress of resident plants with *no apparent change* in soil resource availability (Figure 1c).

Invasion-induced reductions in the availability and provisioning of soil nutrients and water can leave unique physiological signatures on native plants (Figure 2). In response to invasion-induced resource limitations, native plants can change their morphological, physiological, and internal anatomical traits to increase resource use efficiency of leaf tissues. For instance, in response to reduced water availability plants tend to decrease their specific leaf area (SLA) (Poorter *et al.* 2009), allowing for greater leaf-level photosynthetic water use efficiency (WUE) by reducing the surface area from which water is lost (Figure 2). However, SLA shows only a limited response to soil nutrients (Firn *et al.* 2019). Stomatal conductance also decreases with increasing water stress (Prentice *et al.* 2011; Prentice *et al.* 2014; Lin *et al.* 2015), increasing WUE, particularly if plants increase nutrient uptake to support photosynthesis under water

limitation (Wright *et al.* 2003; Wright *et al.* 2005). However, this results in a decrease in photosynthetic nutrient use efficiency (PNUE) under water limitation (Wright *et al.* 2003). Conversely, reduced nutrient availability tends to increase PNUE and decrease WUE (Wright *et al.* 2003). This trade-off leads to the prediction that plants under water stress would have higher nitrogen per leaf area (N_{area}) for a given rate of stomatal conductance (g_s) relative to plants under low water stress (Figure 2). Alternatively, one would expect a decrease in N_{area} at a given g_s with soil nutrient stress. This trade-off has been confirmed in global observations (Paillassa *et al.* 2020), but has not been examined in an invasion context. We expect the optimal combination of photosynthetic traits to shift if invasive species alter the availability or provisioning of one or more soil resources. In this scenario, native plants in the invaded community that are best able to shift their morphological, anatomical, and physiological traits are likely to be the least impacted by invasion.

While physiological responses may help to maintain per-leaf-area rates of photosynthesis, they may only have limited benefit to whole-plant performance (i.e., biomass accumulation and reproduction) if the soil resources necessary to build new tissues are severely limited (Figure 1e). Indeed, biomass responses to soil resource availability are very strong (Wu *et al.* 2011; Harpole *et al.* 2017). This may cause a negative feedback to invasion if invasion-induced reductions in resource availability limit nutrient acquisition by suppressing root growth.

Here, we explore the effects of an allelochemical-producing invader on belowground processes and explicitly link these changes to shifts in native plant traits, resource use efficiencies, and growth. Our primary objective was to distinguish between altered soil resource availability

(depletion or enhancement) versus plant-fungal mutualism disruption as pathways underpinning invasion-induced shifts in native plant traits and performance (Figure 1). The invader we investigated, *Alliaria petiolata* (Brassicaceae), is a biennial herb from Eurasia that produces secondary compounds toxic to AM fungi (Rodgers *et al.* 2008a; Cantor *et al.* 2011). This study leverages a 14-yr long manipulative field experiment, in which *Alliaria* was weeded from one side of five paired plots and was left at ambient densities on the other side of each plot. Our specific aims were to evaluate the extent to which long-term removal of *Alliaria* leads to changes in (1) the availability of key limiting soil resources (including nitrogen, phosphorous, soil moisture), (2) the soil AM fungal community and abundance of AM fungi in native plant roots, (3) shifts in traits and resource use efficiencies of native forest understory perennials, and (4) changes in whole-plant biomass accumulation.

Following the mutualism disruption hypothesis, we predict that the long-term removal of *Alliaria* would increase AM fungal root colonization and alter the AM soil fungal composition. These changes in AM fungal associations would increase soil resource provisioning to the native plant partners, detectable as a decrease in SLA and increase in N_{area} . We expect similar shifts if *Alliaria* directly lowers soil resource availability for native plant species. At the whole-plant level, we expect higher native plant growth in the *Alliaria* weeded treatment than the ambient treatment due to increased soil resource availability or provisioning.

Methods

Study site

Our study site is in Fox Chapel, PA (50.520237, -79.900932) in the Trillium Trail Nature Reserve. The experimental design includes five 14 x 14 m paired plots subdivided in 36 2 x 2 m subplots. Beginning in 2006, we weeded *Alliaria* every spring from the left side of each plot and carried the weeded material offsite. The right side of each plot was left at ambient *Alliaria* field densities, resulting in a split plot design. To prevent seed dispersal and re-infestation of *Alliaria* in subsequent years, we installed temporary mesh barriers between the weeded and ambient sides of the plots prior to *Alliaria* seed maturation that were removed post seed dispersal each year.

Non-native invader

Alliaria petiolata (Brassicaceae) is a biennial allelochemical-producing herb from Eurasia that invades both disturbed environments and forest interiors throughout North America. *Alliaria* produces glucosinolates that undergo hydrolysis when released into soils and are converted to cyanide compounds that inhibit respiratory electron transport. These secondary compounds are toxic to AM fungi (Cantor *et al.* 2011), soil pests and pathogens (Brown 1997), and insect herbivores (Chew 1988; Porter 1994). A derivative of glucosinolates, allyl isothiocyanate (AITC), inhibits AM fungal spore germination and reduces soil respiration, root colonization, and arbuscule formation in plants associated with AM fungi (Stinson *et al.* 2006; Cantor *et al.* 2011; Hale *et al.* 2011; Hale & Kalisz 2012; Hale *et al.* 2016). *Alliaria* invasion often increases soil N, P, Ca, and Mg availability and soil pH (Rodgers *et al.* 2008b; Anthony *et al.* 2017).

Our previous work demonstrated that *Alliaria* can have cascading negative effects on the performance and population growth rate of AM dependent understory plant species (Bialic-Murphy *et al.* 2019). We also previously found that *Alliaria* alters the diversity of native plant

communities by reducing the abundance of mycorrhizal plant species, with no subsequent changes in non-mycorrhizal plant species (Roche *et al.* 2020).

Focal native species

The focal natives we used for this study are *Arisaema triphyllum* (L.), *Trillium erectum* (L.), and *Maianthemum racemosum* (L.). These species are long-lived understory forest perennial herbs common in eastern North American temperate forests. The focal species have belowground rhizomes with coarse root systems that lack root hairs and form root-AM fungal symbioses and produce aboveground stems and leaves that senesce annually (Brundrett & Kendrick 1988). The timing and duration of aboveground phenology (period of active photosynthesis) differs among the focal species, with aboveground emergence through senescence spanning April to July for *Trillium*, May to September for *Maianthemum*, and April to August for *Arisaema* (Heberling *et al.* 2019a; Heberling *et al.* 2019b). Leaves fully expand prior to canopy closure for *Trillium* but continue to expand for up to a month following canopy closure for *Arisaema* and *Maianthemum*.

Soil samples

To examine the effects of *Alliaria* on abiotic soil resources and AM fungal community composition, two subplots within each paired plot were sampled in June 2018 following Burke *et al.* (2019). To obtain a sufficient amount of soil (50 g wet weight), five to ten soil cores in each subplot were separated into organic and mineral horizons and pooled separately for a total of 20 soil samples (2 *Alliaria* treatments x 2 soil horizons x 5 plots). The depth of each soil layer per soil core was recorded and the cores were separated into the organic and mineral layers following Burke *et al.* (2019).

Soil properties

To determine soil resource availability, phosphate (PO_4^{-3}), ammonium (NH_4), and nitrate (NO_3^-), pH, and microbial biomass carbon (MBC) were extracted within 2 d and soil moisture within 3 d of soil sampling. Soil moisture was determined gravimetrically as the difference between wet soil and dry soil after drying samples at 105°C for two weeks. Soils were extracted in 0.5 M K_2SO_4 at a ratio of 1:5 for extractable PO_4^{-3} , NH_4 and NO_3^- and the nutrients were quantified colorimetrically (Lajitha *et al.* 1999; D'Angelo *et al.* 2001; Doane & Horwath 2003). Soil pH was measured in a 1:2 ratio (w/v) of soil to H_2O slurry. Soil organic matter was estimated at the plot level by loss-of-ignition method and combusting the soil in a muffle furnace at 360°C (David 1988). Microbial biomass carbon (MBC) was estimated using chloroform fumigation and direct extraction following Brookes *et al.* (1985) and expressed as $\mu\text{g C}$ per g of dry soil and is corrected for extraction efficiency (0.45). To assess the length of AM fungal hyphae in the organic and mineral layers, hyphae were extracted from 5 g of soil in 5% sodium hexametaphosphate, filtered through nylon filter (47-mm diameter, $0.45\text{-}\mu\text{m}$ pore size) and stained with acid fuchsin (Kivlin & Hawkes 2011). The stained hyphae were visualized and scored using the grid-line intersect method (Brundrett & Abbott 1995) in 50 grids at 200X and the hyphal length was calculated as mm hyphae per g of dry soil. To capture the average soil properties near the focal native plant roots, we used the average proportion of each soil layer in each subplot to calculate the weighted mean soil properties (i.e., total bulk soil). Overall, the depths of the soil cores before hitting claypan or rock ranged from 2.93 to 15.00 cm, with a mean depth of 11.26 cm.

Soil AM fungal communities

To determine differences in AM fungal composition across *Alliaria* treatments, DNA was extracted from 500 mg of soil using a Power Soil DNA Isolation Kit (MO BIO Laboratories, CA, USA). DNA was quantified using a Qubit Fluorometer and stored at -80°C. To analyze the AM fungal community composition, a nested PCR approach was used to first amplify a 1200 base pair region of the 18S fungal DNA using NL1-NL4 eukaryotic primers (O'Donnell 1993). See Methods S1 for additional details on PCR methods.

AM fungal root colonization

To characterize differences in AM fungal colonization in native plant roots between the *Alliaria* treatments, we collected root samples for each focal native species in June of 2018 (N= 53; 3-13 individuals x 3 native plant species x 2 *Alliaria* treatments). To control for variation in root colonization across plant ontogeny, we restricted our samples to large non-flowering individuals. Roots were cleared and stained following McGonigle *et al.* (1990) and the presence or absence of AM fungal structures (i.e., arbuscules or aseptate hyphae) were counted across 60-125 intersections at 200x.

Leaf-level morphological and physiological traits

To characterize the effect of the *Alliaria* treatments on morphological and physiological traits associated with water and nutrient use efficiency for the focal native understory species, we quantified the instantaneous physiology of a subset of reproductive and non-reproductive plants in 2018 (N= 468; 29-57 individuals x 2 *Alliaria* treatments x 3 species x 2 life stages). We measured the net photosynthetic rate (A_{sat}), and stomatal conductance (g_s) using a Li-COR LI-6400XTR portable photosynthesis system, equipped with a CO₂ control module, 2 x 3 cm leaf

cuvette and a red-blue light-emitting diode (LED) light source (Li-Cor, Lincoln, NE, USA). Measurements were taken at a saturating light level of $800 \mu\text{mol m}^{-2}\text{s}^{-1}$, ambient temperature and humidity, and a reference chamber CO_2 concentration of $400 \mu\text{mol mol}^{-1}$, following Heberling *et al.* (2017). To minimize within-plant variability for *Maianthemum*, we restricted our sampling to either the 2nd or 3rd leaf from the terminal end of the stem following Cornelissen *et al.* (2003) and only used leaves without signs of senescence or damage (e.g. insect herbivory). Specific leaf area (SLA) and leaf carbon and nitrogen concentration were measured on a subset of individuals (11-18 individuals x 2 *Alliaria* treatments x 3 species x 2 life stages). To measure SLA, we collected two to three 5.32 cm^2 leaf tissue samples from each individual and calculated the mean leaf surface area per g dry mass ($\text{cm}^2 \text{ g}^{-1}$). Leaf carbon and nitrogen concentration were measured on dry leaf samples using an elemental analyzer (Costech Inc., Valencia, CA). We used these physiological measurements to calculate water use efficiency (WUE) (A_{sat} / g_s), photosynthetic nitrogen use efficiency (PNUE) ($A_{\text{sat}} / \text{percent nitrogen} * \text{SLA}$), and nitrogen per leaf area (N_{area}) for a given rate of stomatal conductance (g_s). The mean chlorophyll content (Chl) of three leaflets per plant was measured using a SPAD 502 Chlorophyll Meter (spectrum Technologies, Inc, Aurora, IL, USA); (N=284; 34-57 individuals x 3 species x 2 *Alliaria* treatments x 2 life stages). To standardize our sampling, we chose to measure Chl from the darkest green section of each leaflet. The Chl-sampled individuals are a subset of plants for which the other functional traits were measured and the same plants for which whole-plant performance were measured (below).

Light availability and canopy openness

To test if focal species' trait characteristics were driven by differences in ambient light levels in the *Alliaria* ambient and weeded treatments, we took hemispherical 180° image digital photographs with a Pentax K-50 camera fitted with a Lensbaby™ circular fisheye lens. To take the photographs, the camera was held ~ 80 cm above the forest floor on a tripod in the center of each subplot in which functional trait data were collected. The camera was set to the full wide-angle mode, with the flash and macro setting turned off. To maintain consistent image alignment, we standardized the directionality of each photograph (e.g., top of photograph facing North and left side facing West). Photographs were post-processed and analyzed using Gap Light Analyzer 2.0 software to calculate the gap light index (Frazer *et al.* 1999), a metric of diffuse and direct beam radiation.

Whole-plant performance

To capture the effect of the *Alliaria* treatment on plant growth, we selected N = 501 individuals across the three species and measured aboveground size in June-July in 2018 and 2019. Plant biomass was estimated using species-specific allometric equations previously developed (Brouwer *et al.* 2015; Bialic-Murphy *et al.* 2019; Bialic-Murphy *et al.* 2020).

Statistical analysis

Soil properties

To evaluate the effects of the *Alliaria* ambient and weeded treatment on abiotic soil concentrations of PO_4^{-3} , NH_4 , NO_3 , MBC, and the biomass of fungal hyphae, we conducted univariate analyses for each variable separately using a generalized linear mixed effect model.

To improve normality of the residuals, PO_4^{-3} and soil moisture were square root transformed and pH, NH_4NO_3^- , and MBC were natural log transformed.

Soil AM fungal communities

To characterize differences in alpha diversity between treatments, we calculated the Shannon-Wiener index and Simpson diversity index. To test for significant differences in Shannon-Wiener, we used a linear mixed effect model and for the Simpson index we used a mixed effect model with a beta distribution. To capture differences in the soil fungal community composition between the *Alliaria* treatments based on species abundance, we used a permutation multivariate analysis of variance (PERMANOVA) using the *vegan* package and the *adonis* function

AM fungal root colonization

To quantify differences in the 2018 root colonization rates of AM fungi between the *Alliaria* ambient and weeded treatments, we used a beta regression model (Crawley 2007). For each model, we included the *Alliaria* treatment, the focal native species, and an interaction term as a fixed effect. The response variable for each model was the proportion of arbuscules or aseptate hyphae present across 60-125 fields of view.

Leaf-level morphological and physiological traits

To evaluate the effect of the *Alliaria* treatments on the morphological and physiological traits, we conducted univariate analyses for each trait separately using a linear mixed effects model. The fully parameterized models included the *Alliaria* (ambient or weeded) treatment, the focal native species (*Arisaema*, *Maianthemum*, and *Trillium*), initial plant size (2018), and a treatment

by species interaction term as predictor variables. The response variables were A_{sat} , Chl, WUE, g_s , SLA, PNUE, N_{area} , and N_{area}/g_s . Examining differences in morphological and physiological traits for the reproductive life stage was not possible for *Arisaema* because few individuals flowered in 2018, so the morphological and physiological traits for reproductive and non-reproductive life stages were analyzed separately. To improve nonnormality of the residuals, we log transformed PNUE, WUE, and g_s .

Light availability and canopy openness

To test for differences in light availability between *Alliaria* ambient or weeded treatment, we calculated the gap light index and applied a generalized linear model. The fully parameterized model included the *Alliaria* treatment as the predictor variable and the total diffuse and direct beam radiation as the response variable.

Whole-plant performance

To examine if the *Alliaria* treatments influenced plant growth of our focal native species, we used a linear mixed model. To improve nonlinearity, size at time t_{2018} and t_{2019} were log transformed. The fully parameterized models included the *Alliaria* (ambient and weeded) treatment and initial plant size as fixed effects.

All statistical analyses were conducted in R v. 3.4.3 (R Development Core Team 2013). Generalized linear models were fit using the `glm` function and generalized linear mixed models were fit using the `lmer` and `glmer` functions in package `lme4` (Bates *et al.* 2009). To account for the nested experimental design and non-random spatial structure, we included

treatment nested within plot as a random factor in our regression models. To test for significant main effects and interaction terms, we used backward stepwise regression. Non-significant interactions and main effects were dropped sequentially, removing non-significant interaction terms first. Comparisons between the fully parameterized models and reduced models were made using a likelihood ratio test. Significant differences were determined using type III analysis of deviance for interactions and type II for main effects, using the `Anova` function in the `car` package (Fox *et al.* 2007). To identify significant difference between factor levels, we calculated differences of least squares means and confidence intervals using the `lmerTest` package and the `diffLsmeans` function (Kuznetsova *et al.* 2017).

Results

Soil properties

We found that hyphal length of AM fungi (i.e., aseptate hyphae) in the organic soil layer was lower in *Alliaria* weeded plots compared to ambient plots ($P = 0.047$; Figure 3). However, this effect disappeared in bulk soils ($P = 0.093$). Regardless of whether the organic and mineral layers were analyzed separately or as a weighted mean (bulk soils), no other soil properties differed between the *Alliaria* treatments ($P > 0.050$, Figure 3).

Soil AM fungal communities

In the organic soil layer, AM fungal Shannon-Wiener diversity was significantly lower in the weeded treatment than the ambient treatment ($P = 0.039$; Figure 4b), but all other measures of AM fungal diversity did not vary between treatments ($P > 0.050$). Soil AM fungal community

composition in the organic layer also did not vary between *Alliaria* treatments ($R^2 = 0.074$, $P = 0.377$; Figure 4a).

In the mineral soil, neither AM fungal Shannon-Wiener diversity ($P = 0.778$) nor Simpson index ($P = 0.160$) varied between the *Alliaria* treatments (Figure 4e, f). However, the soil AM fungal community composition in the mineral layer differed between treatments ($R^2 = 0.168$, $P = 0.023$; Figure 4d).

AM fungal root colonization

Colonization of native plant roots by arbuscules ($P < 0.001$; Figure 5a) and aseptate hyphae ($P = 0.009$, Figure 5d) in *Arisaema* was higher in the *Alliaria* weeded treatment than the ambient treatment. For *Maianthemum*, there was no difference between treatments in the root colonization by arbuscules ($P = 0.335$; Figure 5b) or aseptate hyphae ($P = 0.184$; Figure 5e). Similarly, there was no difference between treatments in the root colonization by arbuscules ($P = 0.608$; Figure 5c) and lower colonization by aseptate hyphae ($P = 0.002$; Figure 5f) in the weeded treatment for *Trillium*.

Light availability and canopy openness

Overall, total diffuse and direct beam radiation did not vary between the *Alliaria* treatments ($P = 0.717$). These results indicate morphological and physiological trait differences between treatments were not driven by variation in canopy openness as measured by diffuse and direct beam radiation.

Leaf-level morphological and physiological traits

For the non-reproductive life stage, N_{area} was consistently higher (7.8%) ($P = 0.023$, Figure 6a) in the *Alliaria* weeded treatment as compared to the ambient treatment. There was also a lower g_s in the *Alliaria* weeded treatment than the ambient treatment for one species (*Arisaema*; $P < 0.028$; Figure 6b), but no change in g_s between treatment for *Trillium* ($P > 0.505$; Figure 6b) or *Maianthemum* ($P > 0.373$; Figure 6b). Combined, these effects resulted in a higher N_{area} to g_s ratio in the *Alliaria* weeded treatment compared to the ambient treatment for all three native plant species ($P = 0.018$; Figure 6c). Light-saturated net photosynthesis (A_{sat}) was lower (20%) in the *Alliaria* weeded treatment than the ambient treatment for all three native plants ($P = 0.044$; Figure 6d), which, combined with the N_{area} response, resulted in a lower PNUE (16%) in the *Alliaria* weeded treatment than the ambient treatment ($P = 0.013$; Figure 6e). The A_{sat} and g_s responses reduced WUE for *Arisaema* ($P = 0.002$), but not for *Maianthemum* ($P = 0.282$) or *Trillium* ($P = 0.298$) in the weeded treatment (Figure 5f). SLA was higher in the *Alliaria* weeded treatment than the ambient treatment for all three native plants ($P = 0.004$; Figure S1). Leaf chlorophyll content (Chl) did not differ between treatments for any of the native species ($P = 0.150$; Figure S1).

For the reproductive life stage, A_{sat} ($P = 0.004$) and PNUE ($P = 0.019$) were lower in the weeded versus ambient treatment for *Maianthemum*. All other morphological and physiology traits did not differ between treatments for any native plant species ($P > 0.050$).

Whole-plant performance

Plant growth differed across plant ontogeny, with smaller individuals growing faster than larger individuals ($P < 0.001$). However, the change in plant size from 2018 to 2019 did not differ between treatments for any of the focal native plant species ($P > 0.050$; Figure S2).

Discussion

Invasive plants are commonly superior resource competitors, reducing soil nutrients to lower levels than can be tolerated by native species. It is becoming increasingly clear that invasion can also disrupt plant-fungal symbionts and reduce nutrient and water provisioning. What so far has remained unclear is the extent to which these invasion-induced changes in belowground dynamics impact aboveground plant traits and performance. Here we provide empirical support for the mutualism disruption hypothesis as a mechanism of invasion success, demonstrating aboveground changes in native plant traits and performance are driven by the disruption of belowground root-fungal symbionts. Specifically, we found no apparent differences in soil nutrient availability after 14-years of *Alliaria* removal. These results are similar to previous studies, which found little evidence of recovery in abiotic soil properties following *Alliaria* removal (Anthony *et al.* 2019; Burke *et al.* 2019). Unlike abiotic soil resources, we find lower AM fungal abundance in the roots of *Arisaema* and higher soil fungal diversity in the *Alliaria* ambient treatment. These findings are congruent with previous works, which found plant invasion increased microbial species richness (Kivlin & Hawkes 2011; Anthony *et al.* 2017; Anthony *et al.* 2019). Together these results suggest that the main mechanism of *Alliaria*'s impact on native plant performance is mediated through resource provisioning, and not resource availability.

415 Invasion-induced reductions in soil resource provisioning via mutualism disruption should shift
416 native plant traits linked to carbon and nutrient economies, particularly if resources are limiting.
417 Under nutrient stress, plants may adjust their trait expression to maintain similar leaf-level
418 photosynthetic rates by trading efficient use of abundant resources for that of limiting resources
419 (Wright *et al.* 2003). For the first time, our results from our 14-yr experiment support these
420 predictions in an invasion context. We detected divergent morphological and physiological traits
421 for all three focal native species in the weeded and ambient treatments. Specifically, plants in the
422 ambient treatment adopted a resource conservative strategy (low nitrogen concentration and
423 specific leaf area) (Funk 2013). We also find evidence that plants in the *Alliaria* ambient
424 treatment had a higher cost of nitrogen uptake than plants in the *Alliaria* weeded treatment, as
425 indicated by the greater PNUE and lower ratio of N_{area} to g_s , consistent with previous results
426 across nutrient availability gradients (Paillassa *et al.* 2020). For one native
427 species, *Arisaema*, there was evidence of differential trait investment that increased PNUE and
428 decreased WUE, as would be expected if nutrient availability was more impacted than water
429 availability by *Alliaria* invasion (Figure 2) (Wright *et al.* 2003). Altogether, this evidence
430 demonstrates that plants in *Alliaria* invaded sites can maintain carbon fixation by expending
431 more water to compensate for the disruption of root-fungal symbionts and reduced nutrient
432 provisioning. More generally, these results provide some of the first evidence that invasion may
433 drive native plants toward novel regions of their trait space to maintain optimal carbon and
434 nutrient economies. Furthermore, our results suggest trait flexibility underlies a species' ability
435 to withstand invasion-induced resource limitation and may explain the observed variation in
436 mycorrhizal dependency of native plants for maintaining biomass accumulation (Rodgers *et al.*
437 2008a). However, more research is needed to determine if these changes in plant traits are simply

driven by a sheer decrease in the abundance of beneficial root-fungal associations or a shift in the rate of resource provisioning by effective fungal partners.

At the whole-plant level, we found high variability in plant growth with small plants increasing in size and large plants decreasing in size on average. Pronounced shrinkage of large individuals is common for species with a high degree of modularity, such as our focal natives, and can be adaptive for delaying senescence and preventing mortality during low resource years (e.g., drought years) (Horvitz & Schemske 1995; Salguero-Gómez & Casper 2010). We also found no difference in biomass accumulation between the *Alliaria* treatments for our focal native species. These results are congruent with our previous work, in which we found no effect of the *Alliaria* treatment on *Trillium*'s biomass accumulation over a six-year period (Bialic-Murphy *et al.* 2019). Despite no treatment differences in biomass accumulation, we did find a decreased probability of *Trillium*'s reproduction (flowering and fruiting), seedling establishment, and survival between the *Alliaria* treatments (Bialic-Murphy *et al.* 2019). Those changes in demographic performance translated to a significant decrease (2.3-3.5%) in *Trillium*'s time-averaged population growth rate (Bialic-Murphy *et al.* 2019). Our results differ from studies on woody species, which found *Alliaria* invasion suppressed biomass accumulation at the seedling stage (Stinson *et al.* 2006). These mixed results suggest invasion may have more pronounced effects on plant growth at the seedling stage and/or may differ among herbaceous versus woody species. The disruption of root-fungal symbionts by *Alliaria* may also induce trade-offs in resource allocation between life history traits (i.e., size at first reproduction and life time reproductive success) via changes in demographic performance. Globally, our findings empirically demonstrate that some plants can minimize the impacts of invasion in terms of

biomass accumulation by employing alternative trait strategies. However, the costs of invasion-induced resource limitation may have stronger negative effects on other demographic rates, as seen for *Trillium* (Bialic-Murphy *et al.* 2019). By allocating limiting resources to maintain biomass accumulation, plants may decrease the availability of resources needed for future reproductive output (i.e., the Principle of Allocation)(Levins 1968; Obeso 2002). These findings emphasize the need to integrate perspectives from life history theory and ecophysiology to better understand and predict species resistance to invasion-induced shifts in belowground dynamics.

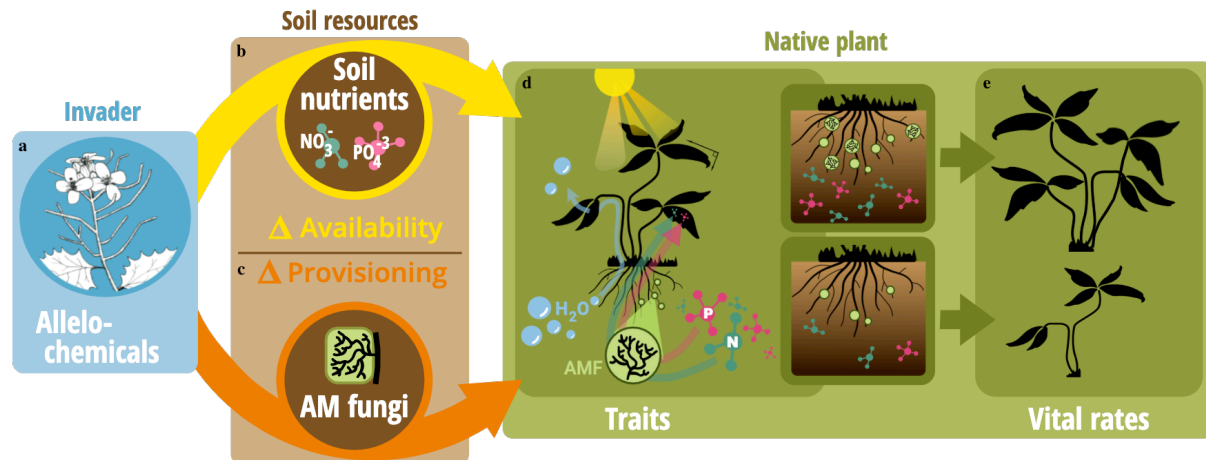


Figure 1: Invasive plants can lead to resource limitation through the depletion of soil resources (panel b) or the disruption of mutualistic interactions respectively (panel c). These alternative or concurrent pathways of invasion-induced resource limitation can be detected as a shift in native plant traits linked to their carbon and nutrient economies (panel d). Plants that can adjust their trait space to maintain leaf-level photosynthetic output are likely to be the least impacted by invasion. However, metrics of whole-plant performance (i.e., survival, growth, and reproduction) can be constrained if resources necessary to build new tissues are significantly limited (panel e).

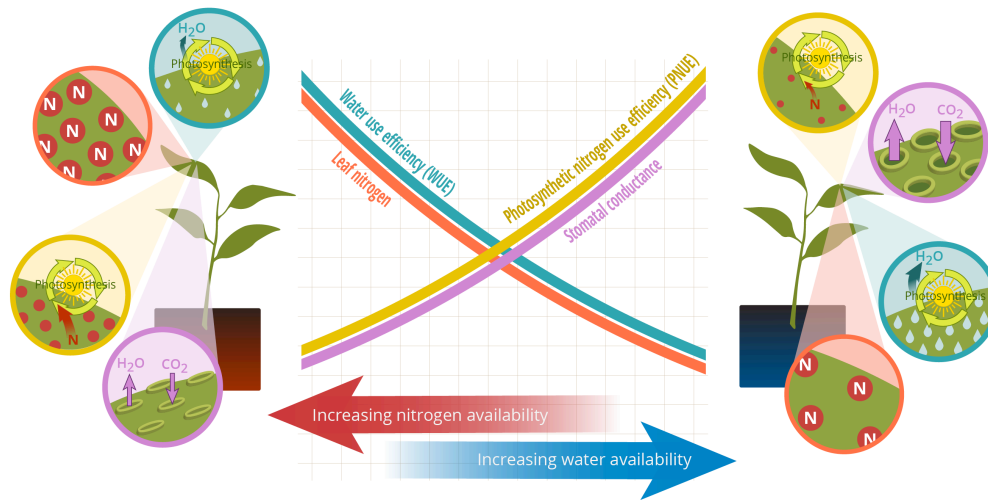


Figure 2: Plant responses to altered nutrient and water availability and/or provisioning. Plants tend to increase stomatal conductance and decrease leaf nitrogen in low nutrient environments and vice versa in low water environments. In order to maintain similar leaf-level photosynthetic rates in low resource environments, plants can trade the efficient use of abundant resources for that of limiting resources. For example, plants in nutrient limited environments can increase PNUE and decrease WUE. These tradeoffs lead to the prediction that plants under high nutrient stress will decrease leaf nitrogen per area at a given stomatal conductance.

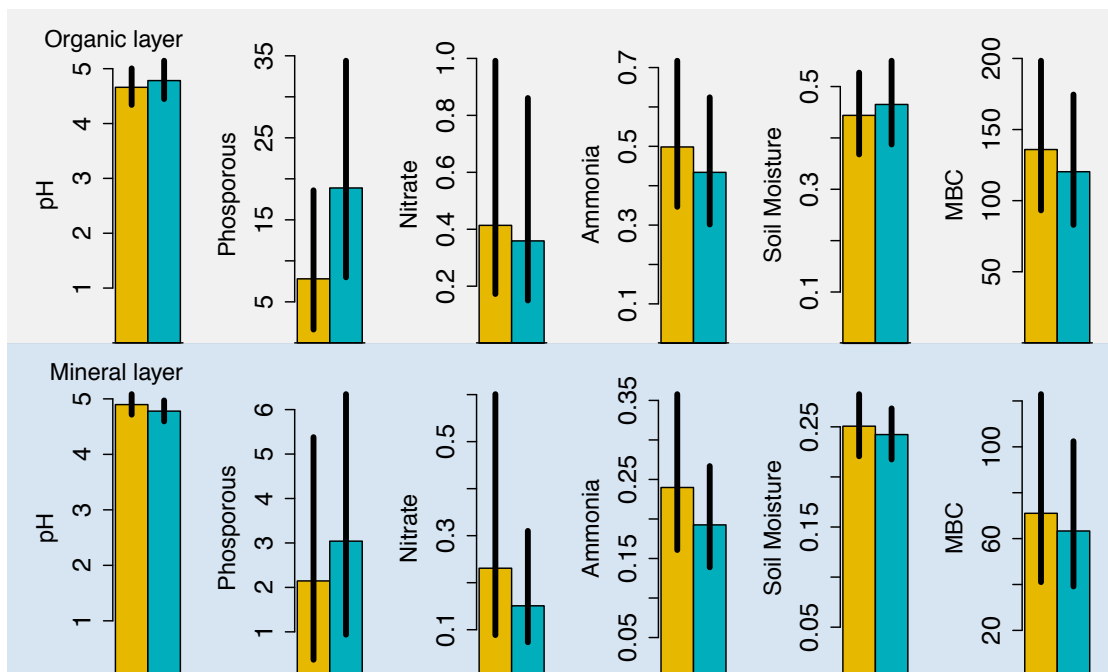


Figure 3: Soil properties in the organic (top) and mineral (bottom) layers. All soil properties were non-significant between the ambient (gold) and weeded (teal) treatments at $P = 0.05$.

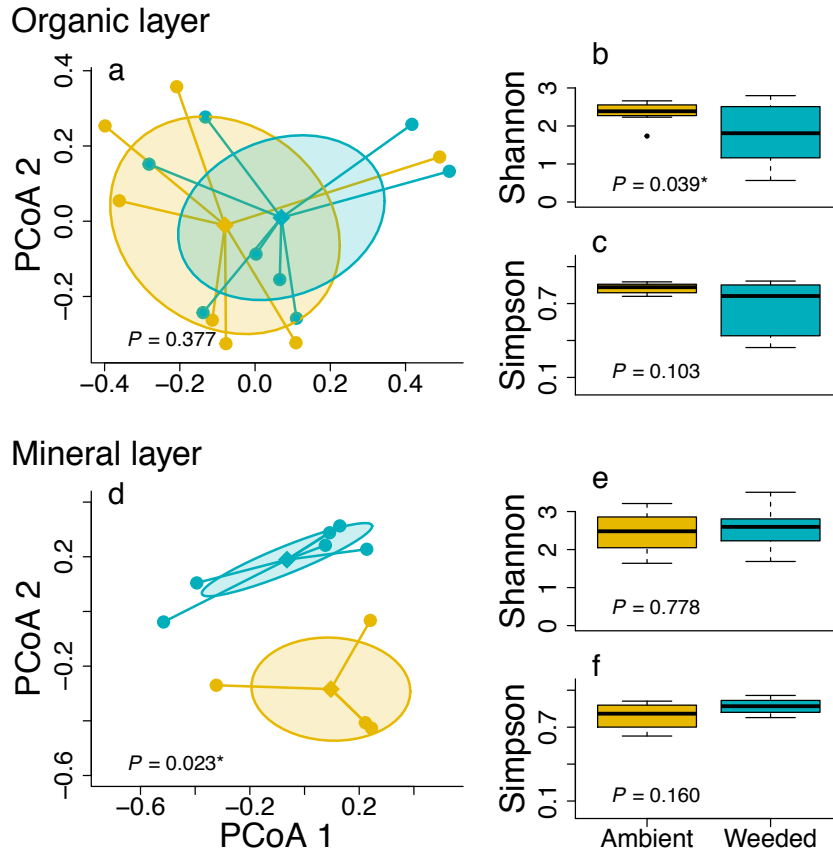


Figure 4: Comparison of *Alliaria* treatment effects (ambient or weeded) on soil fungal community beta (a, d) and alpha diversity (b, c, e, f) for two soil layers: organic (top) and mineral (bottom). The Principal Coordinates Analysis graphs (left) illustrate the similarity or dissimilarity (beta diversity) of the soil fungal community between treatments based on species abundance. The graphs to the right show differences in soil fungal Shannon-Wiener diversity and Simpson Index between the ambient (gold) and weeded (teal) treatments.

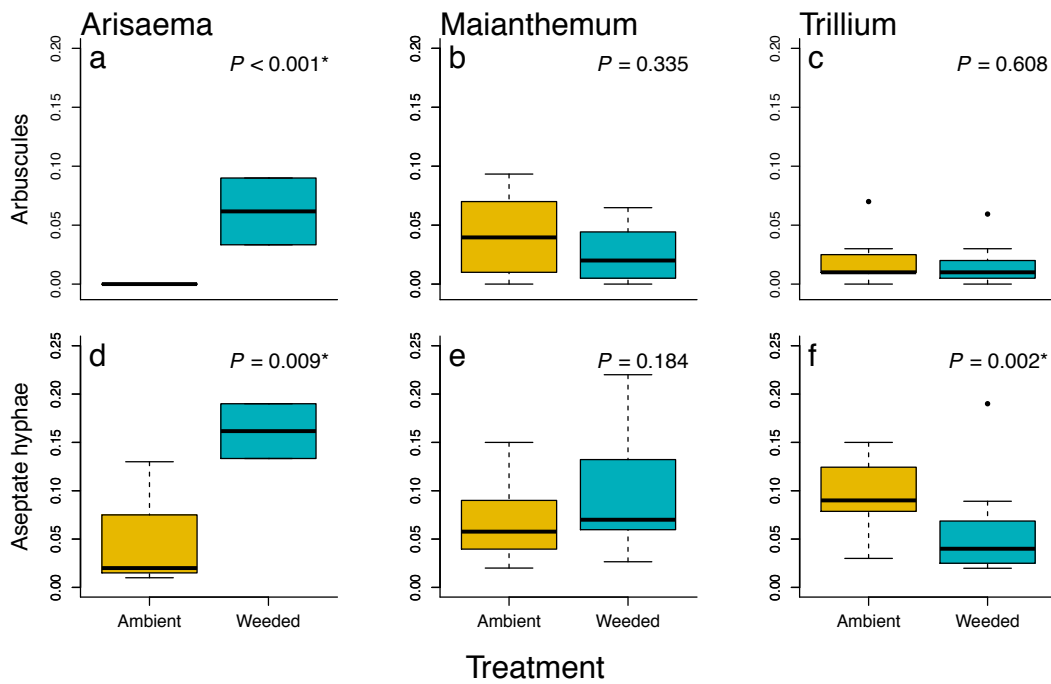


Figure 5: Root colonization of the focal native perennials (*Arisaema*, *Maianthemum*, and *Trillium*) in the *Alliaria* ambient and weeded treatments in 2018. The response variable was the proportion of arbuscules or aseptate hyphae present across 60-125 fields of view.

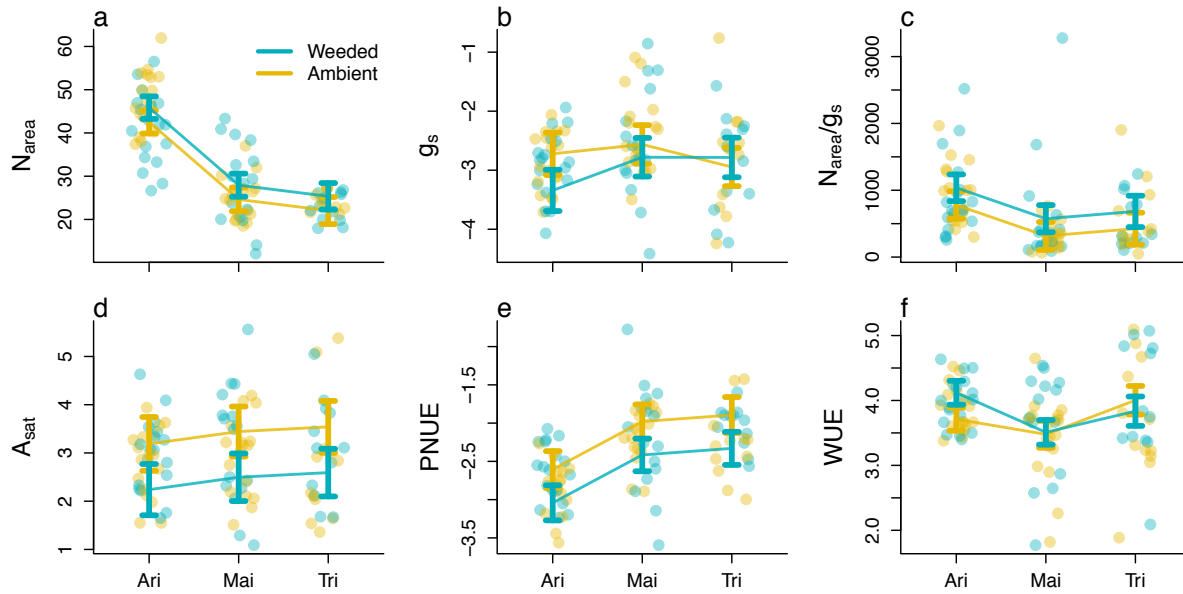


Figure 6: Physiological traits and resource use efficiencies for the non-reproductive life stage in the *Alliaria* weeded (teal) and ambient (gold) treatments. The interaction term between the *Alliaria* treatment and species is significant at $P = 0.05$ for WUE and g_s . The main effect of treatment is significant for A_{sat} , PNUE, N_{area} , and N_{area}/g_s .

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