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Research article

Invasion-mediated mutualism disruption is evident across heterogeneous environmental conditions and varying invasion intensities

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The impact of a biological invasion on native communities is expected to be uneven across invaded landscapes due to differences in local abiotic conditions, invader abundance, and traits and composition of the native community. One way to improve predictive ability about the impact of an invasive species given variable conditions is to exploit known mechanisms driving invasive species' success. Invasive plants frequently exhibit allelopathic traits, which can be directly toxic to plants or indirectly impact them via disruption of root symbionts, including mycorrhizal fungi. The indirect mechanism – mutualism disruption – is predicted to impact plants that rely on mycorrhizas but not affect non-mycorrhizal plant species. To assess whether invader-driven mutualism disruption explains observed changes in native plant communities, we analyzed long-term (1998–2018) plant cover data from forest plots across the state of Illinois. We evaluated native plant communities experiencing a range of abundance of invasive allelopathic garlic mustard *Alliaria petiolata* and varying environmental conditions. Consistent with the mutualism disruption hypothesis, we showed that as garlic mustard abundance increased over time in 0.25 m^2 sampling quadrats, the abundance of mycorrhizal plant species decreased, but non-mycorrhizal plant species did not. Over space and time, garlic mustard abundance predicted plant abundances and diversity at the quadrat level, but this relationship was not present at a larger scale when quadrats were aggregated within sites. Garlic mustard's impact on the plant community was highly localized, yet it was as important as abiotic variables for predicting local plant diversity. We showed that garlic mustard abundance was a key predictor of patterns of plant diversity across invasion intensity and environmental heterogeneity in a way that is consistent with mutualism disruption. Our work indicates that the mutualism disruption hypothesis can provide generalizable predictions of the impacts of allelopathic invasive plants that are evident at a broad spatial scale.

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Introduction

The potential ecological impacts of invasive species on populations, communities, or ecosystems are notoriously difficult to predict (Hulme et al. 2013, Ricciardi et al. 2013) partly due to considerable variation in responses of native communities to invasions. Based on how the traits of the resident species within that community interact with those of the invader, the invader might be prevented from establishing (biotic resistance; (Levine et al. 2003), establish but have a negligible impact on the recipient community (MacDougall et al. 2009), or establish and have a large impact (Hejda et al. 2009, Vilà et al. 2011, Pyšek et al. 2012). In addition, the abiotic conditions at a particular location may or may not match the invaders' 'physiological optimum', which provides a competitive advantage to either the invasive or the native species (Kestrup and Ricciardi 2009, Ricciardi et al. 2013, Iacarella et al. 2015). Our ability to predict the effect of biotic or abiotic conditions on invasion impacts can be limited if the mechanistic processes underlying those impacts are not well understood (Levine et al. 2003). Knowledge of mechanistic drivers of invasion impact will lead to more accurate predictions of which native species, communities, or geographic locations are more likely to be negatively affected by invasive species and will inform management decisions (Sofaer et al. 2018).

Like many processes in ecology, mechanisms of invasion impacts are likely scale-dependent, so the geographic scale of study may influence the observed strength of the mechanism (McGill 2010). Understanding the spatial scale at which a mechanistic process operates will improve predictions of the locations and strength of invasion impacts. Climate, for example, primarily acts at large spatial extents, influencing the region in which an invasive species might be able to establish and invade (Record et al. 2018). However, interactions between the invasive species and the native community including herbivory, competition, or mutualism, may affect the abundance or impacts of an invader on the native community more strongly at small spatial extents and fine spatial grains due to the localized nature of physical species interactions at small scales (Wiens 2011, Wisz et al. 2013).

A mechanistic understanding of invasive species impacts and the spatial scale of those impacts can improve how we anticipate, manage, and mitigate their effects. For example, the invasive annual grass, cheatgrass *Bromus tectorum*, increases fire frequency in ecosystems with historically low fire frequency by increasing connectivity of fine fuels and rapidly re-establishing post-fire, preventing recovery of less fire-adapted native species (Brooks et al. 2004, Bradley et al. 2018). These traits of cheatgrass interact with those of the host communities to lead to mechanistic predictions: impacts are greatest where cheatgrass drives a novel disturbance regime. Areas susceptible to increases in fire frequency (i.e. the Great Basin) are likely to experience substantial impacts of cheatgrass invasion. Conversely, locations such as the eastern United States may be less likely to experience large impacts of cheatgrass invasion, regardless of this invader's ability to establish in those locations because low invader abundance and a wetter climate prevent cheatgrass-driven increases in fire frequency. As this example illustrates, understanding the mechanism of impact, the scale of influence of that mechanism, and climatic/regional conditions conducive to the specific mechanism's functioning are important for predicting where and why invaders are expected to have a high impact (Chambers et al. 2014).

The mutualism disruption hypothesis describes an indirect mechanism by which invasive species impact native species by negatively affecting native species' mutualistic partnerships (Hale and Kalisz 2012). The impact of biological invasions on mutualistic interactions is important to understand because some mutualisms are vulnerable to the negative effects of invasive species (Aslan et al. 2013). Disruption of mutualisms is common and tends to have a negative effect on native species (Christian 2001, Brown et al. 2002, Stinson et al. 2006, Traveset and Richardson 2006, 2014, Meinhardt and Gehring 2012, Riginos et al. 2015, Rogers et al. 2017, Grove et al. 2017a), but the full extent and patterns to such threats are unknown (White et al. 2006). Mycorrhizal associations between plant roots and mycorrhizal fungi are common mutualisms that are threatened by invasion (Grove et al. 2017a). Invasive plants can disrupt mycorrhizas by releasing secondary metabolites that are toxic to mycorrhizal fungi in the soil, thereby preventing the exchange of nutrients and water for photosynthetically-derived carbon compounds between mycorrhizal fungi and plants (Cipollini et al. 2012, Hale and Kalisz 2012, Zhang et al. 2021). Notably, allelopathic properties are suspected to be common in invasive plants (Hale and Kalisz 2012, Kalisz et al. 2021), so allelopathic mutualism disruption may also be widespread.

The negative effects of mycorrhizal mutualism disruption on the plant partner are not expected to be uniform across all plant species in an invaded community, providing a basis for *a priori* predictions of the magnitude of invader impacts. Some plant species are non-mycorrhizal and plant species that do form mycorrhizal associations can differ in their dependence on their partner fungi for soil resource acquisition (Johnson et al. 1997, Soudzilovskaia et al. 2020). Thus, if mycorrhizal mutualism disruption in part explains the negative impacts of an allelopathic invader, the response of a particular native plant species to a mutualism-disrupting invader should depend on its requirement for and strength of mycorrhizal associations. Additionally, the abiotic and biotic environment in which the interaction takes place can influence a particular plant species' mycorrhizal dependency

(Suding et al. 2008, Hoeksema et al. 2010, Johnson 2010) and thus its response to an invader's disruption of its mycorrhizal mutualism. Differences in plant community composition and the susceptibility of each community member to allelopathic mutualism disruption may lead to differing community-level responses to mutualism disruption (McCary et al. 2019). Indeed, allelopathic invasion has shown no negative effects on a non-mycorrhizal plant (Cipollini et al. 2008), but strong effects on mycorrhizal tree species (Stinson et al. 2007, Bainard et al. 2009, Meinhardt and Gehring 2012, Grove et al. 2017b). In a long-term experiment in which an allelopathic invader was either present at ambient levels or removed from the plots, the abundance of herbaceous mycorrhizal plant species increased in plots where the invader was removed (Roche et al. 2021). However, non-mycorrhizal plant species abundance were unaffected by invader presence (Roche et al. 2021).

Experimental studies can unveil the mechanistic causes of invasive species impact, but these studies are typically limited in geographic scope. It is rare for a well-supported mechanism of invasion impact to be assessed across the different abiotic and biotic site conditions across an invaded range (Theoharides and Dukes 2007, Goldstein and Suding 2014). In this study we explored the large-scale patterns of *Alliaria petiolata* (Brassicaceae, Bieb., Cavara & Grande, hereafter garlic mustard) impact on native plant communities based on mechanisms of impact that have been determined previously by manipulative experiments. This was a unique opportunity to test a well-formulated hypothesis at multiple spatial scales with a robust long term observational dataset. Garlic mustard releases allelopathic secondary metabolites that are toxic to soil microbes including arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi (Stinson et al. 2006, Callaway et al. 2008, Cantor et al. 2011). At local scales, mutualism disruption by garlic mustard shifts the plant community, with disproportionate negative impacts on plants that associate with mycorrhizal fungi (Stinson et al. 2007, Roche et al. 2021). We therefore expect garlic mustard's impacts on plant communities at landscape scales to follow predictions based on the mutualism disruption hypothesis (i.e. impacts only seen for the portions of the plant community that depend on mycorrhizal fungi).

We tested the impact of garlic mustard on plant communities across time and space using long-term and large-scale plant survey data and asked three main questions: 1) to what extent does mycorrhizal association explain changes in plant species abundance across levels of garlic mustard abundance? 2) does garlic mustard invasion alter plant communities at large geographic and temporal scales in a way that is consistent with mutualism disruption when accounting for varying abiotic conditions? and 3) how strong is the effect of garlic mustard invasion on abundance, richness, and diversity of plant communities when accounting for abiotic variables? We predicted that over time within sites, the abundance of plant species that form mycorrhizal associations would be lower when garlic mustard abundance was high, consistent with allelopathic mutualism disruption, whereas the abundance of non-mycorrhizal plant species would not respond to increases in garlic mustard abundance. Across time and space, we expected abundance and diversity of mycorrhizal plant species to decrease with greater garlic mustard abundance when accounting for variable climatic and soil conditions across a broad geographic scale, whereas the abundance and diversity of non-mycorrhizal plant species would not change with increasing garlic mustard abundance. Since species interactions are anticipated to have effects at smaller spatial scales than climate, we expected that the effects of garlic mustard on abundance and diversity of other plant species would be stronger than the effects of abiotic variables at both the quadrat and the site level, especially at smaller spatial scales.

Material and methods

Study species

Garlic mustard is a Eurasian biennial herb that is invasive in North America. In the first year, garlic mustard exists as a vegetative rosette, then bolts and flowers in the late spring of the second year. This species exhibits allelopathic properties and impacts native plants by disrupting plant-mycorrhizal fungal mutualisms (Stinson et al. 2006, Callaway et al. 2008, Wolfe et al. 2008, Barto et al. 2011, Hale et al. 2011, 2016, Brouwer et al. 2015, Bialic-Murphy et al. 2019). It is a problematic invader of North American forest understories and can form dense stands even in relatively intact forests (Rodgers et al. 2008). Garlic mustard, like many species in the Brassicaceae, produces glucosinolates as secondary metabolites in all of its tissues (Vaughn and Berhow 1999). Glucosinolates are toxic to soil microbes, including AM and EM fungi (Stinson et al. 2006, Callaway et al. 2008, Cantor et al. 2011). Since a large majority of forest understory species form associations with mycorrhizal fungi (Smith and Read 2008), garlic mustard poses a threat to forests across its invasive range.

Long-term observational dataset

We used data from the Illinois Critical Trends Assessment Program (CTAP) of the Illinois Natural History Survey (Carroll et al. 2002) to assess the effects of garlic mustard and mutualism disruption on plant communities across the state of Illinois. This program was established to quantify the conditions and ecological trends of three terrestrial plant habitat types (forests, wetlands, grasslands) in Illinois. We used plant survey data from the CTAP forest ground cover sites collected from 1998 to 2018 (Fig. 1). Sites were resampled on a five year rotation, meaning that ~ 1/5 of the plots were surveyed each year. If a site no longer met the CTAP criteria for inclusion in the monitoring program when resurveyed, a new, unassociated site elsewhere in the township was established to replace it.

We used the species-specific ground cover data (<1 m in height) for this study because it has been established that

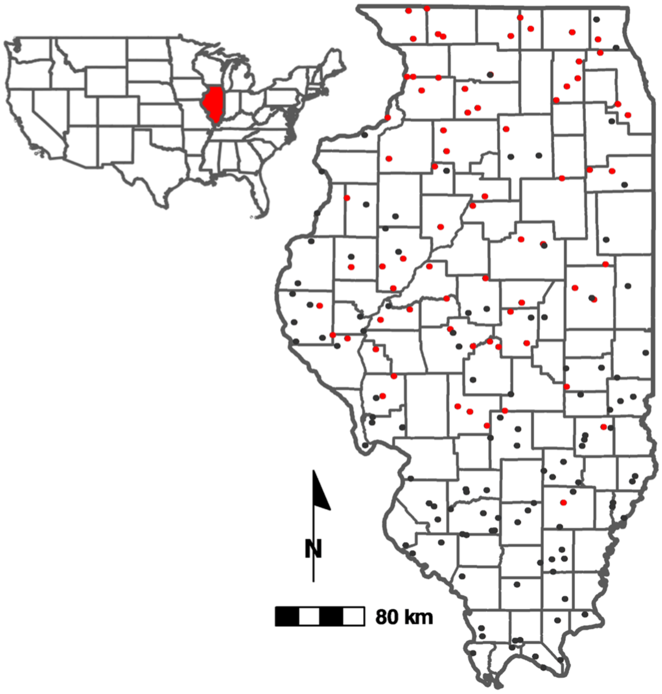

Figure 1. Map of 186 Critical Trends Assessment Program (CTAP) sites across the state of Illinois, USA. Dots represent forest monitoring sites where data were collected from 1998 to 2018. Black dots indicate sites at which garlic mustard has never been observed. Red dots indicate sites with at least one observation of garlic mustard. Inset map shows Illinois in red within the United States.

mutualism disruption by garlic mustard generally has negative effects on forest understory forbs and tree seedlings that form mycorrhizal associations (Stinson et al. 2006, Callaway et al. 2008, Cipollini et al. 2008, Roche et al. 2021). At each site, ground cover sampling occurred at 30, 0.25 m^2 quadrats distributed every 5 m along three permanently marked 50 m transects (10 quadrats per transect), that radiated out from a randomly selected center point in randomly selected, non-overlapping directions. Ordinal plant cover classes (< 1, 1–5, 5–25, 25–50, 50–75, 75–95 and 95–100%) were recorded for each vascular plant species in each quadrat. Methods are further detailed in Carroll et al. (2002). We used the midpoint of cover classes for our analyses.

We analyzed data both at the quadrat and site levels. We averaged percent cover of each species across all 30 quadrats at each site to create the site-level measures of percent cover per species. We included absences only for those species that had occurred in a site or quadrat in at least one other sampling time point to account for losses or additions of species over time. Since mycorrhizal association types are often consistent within plant families, we used established plant family mycorrhizal associations (Brundrett and Tedersoo 2019), to determine mycorrhizal status (i.e. whether a plant species forms mycorrhizal associations, and if so, with what type of mycorrhizal fungi) of all plant species in the CTAP ground cover dataset. We assigned these plant species to one of four mycorrhizal categories following Brundrett and Tedersoo (2019): AM, facultative AM (fac AM), EM, and non-mycorrhizal (NM). Of the 679 plant species (excluding garlic mustard) in the dataset, we were able to assign 624 of them to a mycorrhizal status category (Supporting information); these were our focal species.

Mean-centered abundance over time

We tested whether the effect of increasing garlic mustard abundance on focal species abundance within a site or quadrat was mediated by the focal plant species' mycorrhizal status. For this analysis, we included only the 69 sites at which garlic mustard was observed at least once (Fig. 1), and that had been sampled more than once. This gave us a 20 year total of 181 513 species observations for quadrat-level data and 16 533 species observations for site-level data. We centered the abundance (percent cover) of each focal plant species around the site- or quadrat-level mean abundance for that species. Mean-centering temporal data reveals changes in percent cover of focal species within a site over time (van de Pol and Wright 2009). A focus on changes in abundance of each species within sites isolates the effects of increasing garlic mustard abundance over time from abiotic and biotic conditions that differ over space. Since biotic effects are predicted to be generally stronger at smaller scales (Wiens 2011, Wisz et al. 2013), we analyzed the data averaged across quadrats within each site (site-level analysis) and then separately with 0.25 m^2 sampling quadrat-level data. For both scales, we used mean-centered focal species percent cover as the response variable, including data from all focal species in each model with the interaction between garlic mustard abundance and mycorrhizal status as a fixed effect. We predicted that higher levels of garlic mustard would lead to steeper declines in the abundance of focal species that form mycorrhizal associations at both scales. Our models included random effects of focal plant species and of site, or quadrat within site (for site- and for quadrat-level analyses respectively).

Abundance and diversity over time and space

We assessed the effects of garlic mustard across time and space and the effect of abiotic variables on plant diversity metrics relative to the impact of garlic mustard abundance. We calculated summed abundance, species richness, Pielou's evenness, Shannon diversity and inverse Simpson diversity across all species, and for each mycorrhizal status category separately. We acquired bio-climatic data from CHELSA (Climatologies at High resolution for the Earth's Land Surface Areas) at 30 arc sec. resolution (Karger et al. 2017) and soil variables including net primary productivity (NPP) at 10 arc min. resolution (Foley et al. 1996), soil carbon and pH at 5 arc min. resolution (Global Soil Data Products CD-ROM Contents (IGBP-DIS), data set available online (http://daac.ornl.gov) from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA 2014), and percent soil clay at 30 arc sec. resolution (Hengl et al. 2014). From those datasets, we extracted values for each abiotic variable at each site. We included climatic and soil resource variables as covariates in this analysis across space and time because climatic and soil conditions are expected to affect plant abundance and diversity. Therefore, we included these covariates in the models to account for these differences in climatic and soil conditions across the state of Illinois. In these analyses, we used the 59 sites that had been sampled four or more times regardless of whether garlic mustard had been observed. To test for effects of garlic mustard abundance on community metrics, we looked at both the garlic mustard abundance at a sampling date and garlic mustard abundance at the previous sampling date (i.e. five years prior). We included both the current and previous garlic mustard abundance in the models to account for lag effects (Crooks 2005) of garlic mustard abundance in previous years. Since the effects of garlic mustard are long-lived and recovery of mycorrhizal fungal and the plant communities can lag (Lankau et al. 2014, Brouwer et al. 2015, Roche et al. 2021), we anticipated that previous garlic mustard abundance would also have a negative relationship with the current mycorrhizal plant community. We also expected that that the effects of previous garlic mustard abundance would be weaker than the effects of current garlic mustard abundance. We calculated pairwise Pearson correlations between all abiotic variables and removed variables that were highly correlated (absolute value of r > 0.7). Final covariate sets included 10 total abiotic variables, garlic mustard abundance, and previous garlic mustard abundance. We estimated separate models with site- and quadrat-level plant community data for each mycorrhizal status group. We included either site or quadrat within site as random effects in their respective models to account for non-independence of repeated sampling over time. Since EM plant species were uncommon, we were unable to fit models for that mycorrhizal category at the quadrat level.

All statistical analyses were conducted using R ver. 3.6.2 (www.r-project.org). Linear models were fit using the ‘`glmmTMB`’ package ver. 0.2.3 (Brooks et al. 2017) and model fits were assessed in ‘`DHARMa`’ ver. 0.2.6 (Hartig 2016). All residuals met assumptions for general linear models. We calculated diversity metrics using the ‘`vegan`’ package ver. 2.5–6 (Oksanen et al. 2019). Pearson correlations were calculated using the ‘`stats`’ package in base R (www.r-project.org). Linear model results were based on Wald chi-squared tests and considered significant when $p < 0.05$. We used Type III sum of squares for interaction terms and Type II sum of squares when interaction terms were not tested or were not significant. Variables in time and space analyses were standardized (mean = 0, SD = 1) for ease of comparison across variables on different scales.

Results

Mean-centered abundance over time

At the site level, an increase in garlic mustard abundance was not associated with a change in total percent cover of focal plant species (Fig. 2a; $\chi^2(1) = 0.07$, $p = 0.78$). However, within a sampling quadrat (0.25 m^2), higher garlic mustard abundance was strongly associated with lower abundance of other plants ($\chi^2(1) = 24.58$, $p < 0.001$). There was a weak but non-significant interaction between garlic mustard abundance and mycorrhizal status for quadrat-level data ($\chi^2(3) = 6.17$, $p = 0.10$), but not for the site-level data. Due to small sample sizes in the facultative AM and EM groups, we retested this

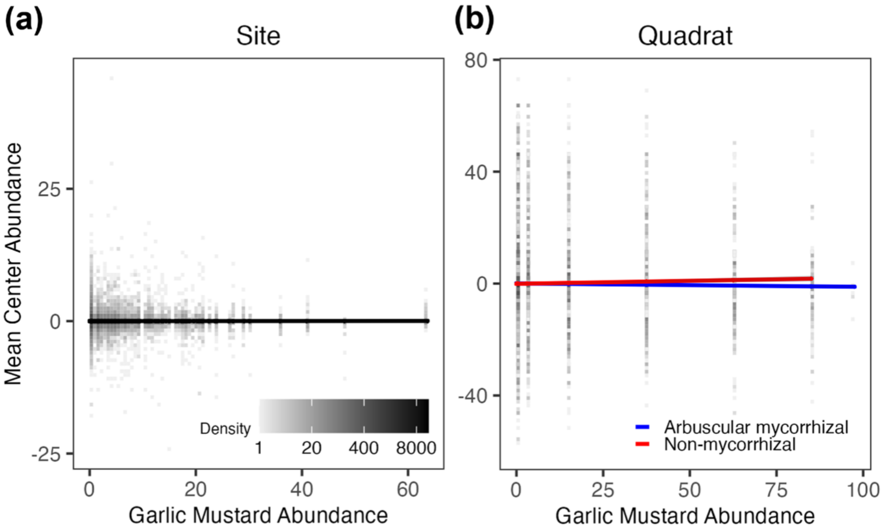

Figure 2. Impact of garlic mustard *Alliaria petiolata* abundance on the mean-centered abundance of other plant species at the (a) site or (b) sampling quadrat (0.25 m^2) level over time. Site-level mean centered abundance (a) was not associated with garlic mustard abundance ($p = 0.78$). With quadrat-level data (b), there was a significant interaction between garlic mustard abundance and mycorrhizal status ($p = 0.01$). A mean centered abundance below zero indicates that the abundance of that species was below the mean for that site or quadrat, whereas a positive effect of garlic mustard would have been above zero. Solid lines are fitted from model outputs, surrounded by model-estimated standard error in gray (smaller than the line symbols). Bins in grayscale represent the density of observations at either the site (a) or quadrat (b), darker bins indicate a higher density of observations.

interaction for the quadrat-level data after removing plant species with facultative AM and EM mycorrhizal statuses. With this reduced model, there was a significant interaction between garlic mustard abundance and mycorrhizal status (Fig. 2b; $\chi^2(1)=6.04$, $p=0.01$), such that with each 1% garlic mustard cover increased within a plot, the AM species decreased by 0.01% in mean centered abundance, and the abundance of non-mycorrhizal plants (excluding garlic mustard) increased by 0.03%. We reported the results of both the full and reduced models here for transparency.

Abundance and diversity over time and space

Garlic mustard had significant associations with focal plant abundance and diversity at the quadrat scale but not at the site scale (Fig. 3, Supporting information). At the quadrat level, higher garlic mustard abundance was associated with decreased abundance and diversity of the focal plant community (Fig. 3b). At the site level, garlic mustard abundance was never a significant predictor of focal species abundance or diversity, but previous garlic mustard abundance was positively associated with site-level abundance of all species (Fig. 3a). Climate and soil variables were important predictors of abundance and diversity of the focal plant community at both spatial scales, however the variables that were important for each model differed between site- and quadrat-level data (Fig. 3). As predicted, garlic mustard abundance was never associated with a change in the abundance or diversity of non-mycorrhizal plant species at the site level (Fig. 3a). For non-mycorrhizal plant species at the quadrat level, an increase in garlic mustard abundance was significantly positively associated with abundance, and significantly negatively

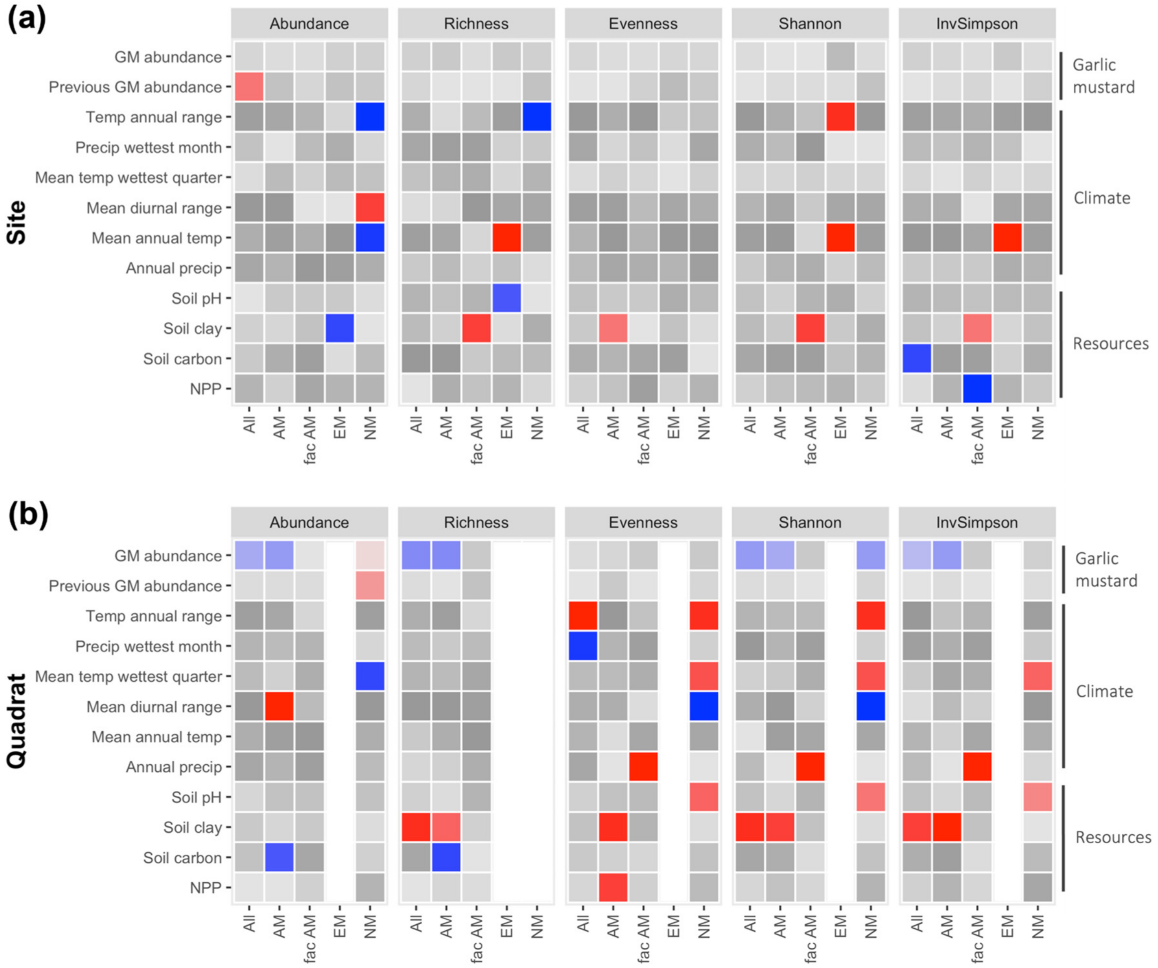

Figure 3. Heatmap showing model estimates (coefficients) from a total of 44 models explaining five plant diversity metrics (abundance, evenness, richness, Shannon diversity and inverse Simpson diversity) for five mycorrhizal status groups of plant species (All species (All), arbuscular mycorrhizal (AM), facultative AM (fac AM), ectomycorrhizal (EM), and non-mycorrhizal (NM)) at the (a) site level and (b) sampling quadrat (0.25 m^2) level. Darker colors indicate a higher rank order of the absolute value of estimated coefficient within each model (all covariates were standardized). Red colors indicate a positive, significant effect, blue colors indicate a negative significant effect, and gray colors indicate that the predictor was not significant at $p=0.05$. Variables are organized by type (garlic mustard (GM) variables, climate variables and resource variables). White bars in panel b indicate insufficient data to fit a specific model. NPP = net primary productivity. See supporting information for statistical tables and scatterplots for garlic mustard abundance.

associated with Shannon diversity, but was not associated with changes in other metrics of diversity (Fig. 3b).

With quadrat-level data, garlic mustard abundance was often a significant predictor of abundance and diversity of the plant community. For example, at the highest garlic mustard abundances, the estimated abundance of AM plant species at the quadrat level was 23.4% lower than when garlic mustard was not present (Supporting information). When garlic mustard did predict abundance or diversity, climate or resource variables were rarely significant predictors (Fig. 3b). At the quadrat level, for the whole community (All) and AM plant species, increased garlic mustard abundance was significantly associated with decreases in abundance, richness, Shannon diversity and inverse Simpson diversity. The patterns of climate and resource predictors vary drastically between the site and the quadrat levels (Fig. 3). We acknowledge the large number of tests conducted for this analysis, and that some of these responses may have shown a significant result by chance. At the site level, we found 17 significant results when we would expect 15 by chance (exact binomial test, $p=0.59$), whereas we found 36 significant results at the quadrat level which is much higher than the 11.4 we would expect by chance ($p > 0.0001$). For the garlic mustard abundance results alone, at the site level we found zero significant results when we would expect 1.25 by chance ($p=0.64$), and at the quadrat level, we found 10 significant results when we would expect 0.95 by chance ($p > 0.0001$). Thus, we found strong evidence for quadrat- but not site-level effects.

Discussion

Using a powerful 20 year dataset over the state of Illinois, we found that the effects of a mutualism-disrupting invasive plant on plant community abundance and diversity were localized to the quadrat scale. The effect of garlic mustard was consistently stronger when we analyzed data at the 0.25 m^2 sampling quadrat level rather than with site-level data. We showed that as garlic mustard abundance increased within a sampling quadrat, its negative impact on the abundance of other plant species also increased. These results provide support for the hypothesis that the impacts of invasive species are scale-dependent (Powell et al. 2011, 2013); although garlic mustard was associated with low diversity at the quadrat scale, site-level diversity was maintained. At the finest spatial grain, where biotic interactions are likely to be most important, an increase in garlic mustard abundance can increase its impact on the plant community.

The mycorrhizal portion of the plant community showed the strongest negative relationship to garlic mustard abundance, providing support for the mutualism disruption hypothesis. We showed that localized garlic mustard abundance (within 0.25 m^2 quadrats) had a negative effect on quadrat-level abundance and diversity of mycorrhizal plant species over time both within sites and across sites. These patterns of garlic mustard impact are consistent with previous work on the impacts of experimental garlic mustard removal on the plant community (Roche et al. 2021). However, a plant community responding to complete garlic mustard removal (as in Roche et al. 2021) would be expected to show different responses in diversity patterns than one that is responding to naturally varying abundances of garlic mustard (as in this study). For example, in garlic mustard removal plots, decreased evenness was driven by a rapid increase in abundance of annual herbs *Impatiens* spp. following garlic mustard removal (Roche et al. 2021), which we would not expect to see in plant communities in this study experiencing naturally occurring low or zero garlic mustard abundance.

Within quadrats over time, increasing garlic mustard abundance was associated with decreasing focal species abundance. The impact of an invasive species is expected to scale with its abundance (Parker et al. 1999, Sofaer et al. 2018, Bradley et al. 2019). Although high abundances of any one species are expected to decrease abundance of other species in a community, invasive species can have higher per-capita effects than native species due to novel traits or lack of co-evolutionary history with the native community (Pearse et al. 2019). It is therefore notable that the changes in the plant communities reflect the signature impact of mutualism disruption by garlic mustard (i.e. negatively impacting only the mycorrhizal plant community). It is also notable that the signature of mutualism disruption was strong within quadrats over space and time (Fig. 3b), reflecting the consistency of this pattern across heterogeneous environmental conditions. We were unable to assess whether differences in climatic and soil conditions altered relationships between garlic mustard abundance and the focal plant community (i.e. an interaction between garlic mustard abundance and climate and soil variables), but this is an interesting and open question.

Regional factors could lead to geographic differences in per-capita allelopathic effects of garlic mustard on native species. Within the state of Illinois, garlic mustard populations are limited in their southern distribution by high summer temperatures (Merow et al. 2017), populations vary considerably in age with younger populations associated with more southern locales (Lankau et al. 2009), and we know that individual allelochemical production can vary with age, light, and conspecific density (Lankau et al. 2009, Smith 2015, Harris 2018). In addition, abiotic conditions within a microsite are known to influence garlic mustard invasion success (Anderson et al. 2019). Thus, site conditions and climate are known to affect garlic mustard's impact on the native community it invades. Despite the noise introduced by all these factors influencing invasion success across space, we found a small but clear signal of disproportionate impact by garlic mustard on plant species that associate with mycorrhizal fungi. This analysis within sites over time result corroborates our analysis across time and space to indicate that the impact of mutualism disruption can be equal to or greater than that of many other abiotic variables.

Garlic mustard has long been recognized as a regionally important plant invader (Rodgers et al. 2008). Unlike other regionally important invaders, such as cheatgrass, that drive large scale ecological changes from large scale processes, we found hyper-local effects of garlic mustard on the plant community as evidenced by data from 0.25 m^2 quadrats that were consistent across large scales, but also that these effects were masked when data were aggregated within sites. This result aligns with previous work showing the hyper-local (0.25 m^2) impacts of invasive species on species richness, whereas heterogeneity and thus masking of the impacts of invasion, occurs at larger plot-level extents (Chen et al. 2010). Our results are also consistent with theory on the scale of importance of species interactions (Powell et al. 2011, 2013), such that species interactions drive local effects. The Parker equation (Parker et al. 1999), describes the impact of an invasive species as the combination of local impacts over a large geographic area. In line with the Parker equation, we saw that the scale of garlic mustard impact was local, and repeated local impacts were widely prevalent across the state of Illinois. This pattern highlights a critical facet of regionally important invaders: despite high impacts at hyper-local scales, signals of regionally important invaders may not be detectable at macro-ecological scales. Therefore, interpretations of regional invasions with coarse-scale data could unintentionally mask important local impacts of invaders that drive regional patterns (Hillebrand et al. 2018, Price et al. 2018).

Data from the CTAP provides 20 years of plant abundance observations, with repeated measurements at hundreds of sites across the state. Long-term data such as these are invaluable for identifying patterns that simply cannot be captured with short-term experiments more common in ecological studies (Blossey 1999, D'Antonio and Flory 2017). However, there is a necessary trade-off that comes with such sampling breadth, as it is not possible to unequivocally establish mechanistic cause from observational data; it is the body of experimental literature that has established the mechanism. Instead, our work evaluates the spatial and temporal scales at which the mechanism manifests. Previous experimental work found unambiguous signatures of the impacts of mutualism disruption on garlic mustard-invaded plant communities (Stinson et al. 2007, Roche et al. 2021), and our results show similar patterns in the effects of garlic mustard on the resident plant community in sites across Illinois. Another unavoidable limitation of this study is that because sites were sampled every five years, we were unable to capture interannual variation in species abundance. While we did establish that abundance of garlic mustard five years prior sometimes predicted current species abundances, the coarse temporal scale in this study may have obscured any lag effects. Thus, our five-year sample window may not have captured short-term plant community responses to garlic mustard. Instead, this study reflects snapshots of the relationship between plant abundance and diversity and garlic mustard abundance.

A major historical criticism of community ecology is that context dependency plays a large role in determining outcomes so it is impossible to uncover generalizable theories (Lawton 1999). Indeed, conclusions surrounding the effects of garlic mustard on plant communities often vary widely by site (Stinson et al. 2007, Davis et al. 2015, Anderson et al. 2019, Roche et al. 2021). However, our study showed that disruption of mycorrhizal mutualisms, which is known to have a physiological impact on individual mycorrhizal plants, had predictable and broadly generalizable effects that were detectable across the state of Illinois with varying environmental conditions and invasion intensities. We found that garlic mustard abundance was a key predictor of local patterns of mycorrhizal plant diversity and abundance across a large geographic area. Many invasive plants besides garlic mustard exhibit allelopathic traits (Kalisz et al. 2021, Zhang et al. 2021), and have the potential to impact native plant communities in a similar way via mutualism disruption (Hale and Kalisz 2012, Grove et al. 2017a). However, because the effects of these allelopathic species are rarely assessed under field conditions (Zhang et al. 2021), mycorrhizal mutualism disruption by allelopathic plant invaders likely remains an underestimated threat to global plant communities.

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Data availability statement

Data are available from the Dryad Digital Repository https://datadryad.org/stash/dataset/doi:10.5061/dryad.z08kprrjb (Roche et al. 2023). Original data available upon request from https://publish.illinois.edu/ctap-inhs/.

Supporting information

The Supporting information associated with this article is available with the online version.

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