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**Is Context Dependency Imperative to Understanding
the Impacts of Invasive Plants?**

Brendan B. Haile

M.S. in Biological Sciences (Thesis): 2020

Eastern Illinois University

Abstract

Introduced exotic species have a tendency to become invasive and impact local biological communities. Invasions often impact community attributes such as cover and species richness, but these factors may also regulate patterns of invasion. In such cases, impacts may be dependent on the invasion context. We used data from the Buell-Small Succession Study, a long-term permanent plot study in the piedmont region of New Jersey, to document context dependency in invasion. To do this, we analyzed the factors that affected the colonization and growth of four invasive species, *Alliaria petiolata*, *Lonicera japonica*, *Microstegium vimineum* and *Rosa multiflora*, as well as the impacts of these invasions on the community. I did this two ways, one analysis which took temporal context into consideration (change over time) and for comparison, I also documented invasion impacts in a single time snapshot.

In *Lonicera japonica* and *Microstegium vimineum*, it was found that more species rich plots were significantly more likely to become invaded, whereas increased species richness inhibited the likelihood of successful invasion by *Alliaria petiolata*. The establishment of *Rosa multiflora* was not affected by variation in species richness. Species richness and total vegetative cover did not significantly affect the growth/spread within successfully invaded plots. Life forms (trees, forbs, lianas, or shrubs) and co-occurring dominant species were linked to the spread of some invasive species. Species richness of the community was significantly affected by *A. petiolata*, *L. japonica*, and *R. multiflora*, within temporally explicit analyses (change over time). The temporally static analysis indicated that species richness was significantly impacted by each of the four

invaders with some showing marked differences from the temporally explicit analysis. Total vegetative cover was similarly affected by species invasion. In each of these case studies, the context of invasion was necessary in understanding their ultimate impacts. The perceived impacts of invasion may be offset or amplified by the factors which regulate invasion. My data suggest that analyses from single-time studies may provide inaccurate estimates of invasion impacts.

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Table of Contents

Title Page.....	I
Abstract.....	II
Acknowledgements.....	IV
Table of Contents.....	V
List of Figures.....	VI
Introduction.....	1
Methods.....	3
Results.....	8
Discussion.....	12
Conclusion.....	17
Literature Cited.....	19

List of Figures

Figure 1. Invasion trajectories of the four focal invasive species for this study. Data plotted are mean cover of the specified species as a function of age/calendar year. Vertical lines represent the timeframe of invasion, T ₁ (initial) and T ₂ (peak).....	25
Figure 2. The impact of each focal invasive species on the species richness by invasion class from T ₁ to T ₂ . Analyses included only plots that were uninvaded at T ₁ . Data plotted are means ± standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.....	26
Figure 3. The impact of each focal invasive species on the total vegetative cover by invasion class from T ₁ to T ₂ . Analyses included only plots that were uninvaded at T ₁ . Data plotted are means ± standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.....	27
Figure 4. The impact of each focal invasive species on the species richness by invasion class at T ₂ . Analyses included only plots at T ₂ . Data plotted are means ± standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.....	28
Figure 5. The impact of each focal invasive species on species richness by invasion class of both the temporally explicit (T ₁ -T ₂) and static (T ₂) analyses. Data plotted are means ± standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.....	29

Introduction

There are approximately 3,988 non-native plant taxa found in the continental United States (Simpson & Eyler, 2018). Non-native plants may be introduced deliberately for their uses in landscaping or agriculture, providing economic and societal benefits. Agricultural uses of non-native species comprise a significant portion of the United States' food system and have been valued at \$800 billion each year (Pimentel et al., 2005). However, non-native plants may also be introduced accidentally through transportation of soil or as agricultural contaminants (Ibáñez et al., 2009; Pimentel et al., 2005), or may escape cultivation (Mack, 2000; Mack & Erneberg, 2002). Despite the economic value of some non-native species, invasive plants and animals are estimated to have caused environmental and agriculture damage totaling to approximately \$120 billion each year (Pimentel et al., 2005).

Non-native invasive plant species have varying impacts on invaded communities in which they have become established (Banasiak & Meiners, 2009; Parker et al., 1999; Pritekel et al., 2006; Yurkonis et al., 2005), representing ecological costs to invasion. Invasive plants frequently decrease the local species richness of invaded communities (Pritekel et al., 2006; Pyšek et al., 2012; Yurkonis et al., 2005). However, the idiosyncratic nature of each species-community pairing makes the impacts of invasion difficult to generalize (Ibáñez et al., 2009; Pyšek et al., 2012). Similarly, invasive species often reduce total vegetative cover, but some studies have found increased total cover following invasion (Aguilera et al., 2010; Banasiak & Meiners, 2009; Pritekel et al., 2006; Pyšek et al., 2012). Invasive plant species may also shift the availability of limiting soil nutrients such as nitrogen or phosphorous (Aguilera et al., 2010; Parker et al., 1999;

Pyšek et al., 2012), or impact associations with mycorrhizal fungi (Hale et al., 2016; Lankau, 2010) altering the resource uptake of associated species. Given the complexities of species interactions, it is perhaps unsurprising that the impacts of non-native invasive plants vary widely.

Motivated by the documented impacts of non-native invasive plants, much attention has been paid to the factors that facilitate invasion. Species richness is believed to play an integral role in determining the invasibility of a community, due to the existence of open niche space (Lankau, 2010; Mack, 2000; Seastedt & Pyšek, 2011). Invasive species can only invade communities with sufficient availability of soil resources (Lankau, 2010; Seastedt & Pyšek, 2011) and available light (Ibáñez et al., 2009; Lankau, 2010; Yurkonis et al., 2005). In a similar vein, disturbances generally increase the likelihood of invasion by disrupting vegetative cover, increasing the amount of resources available by creating gaps in above and belowground canopies (Ibáñez et al., 2009; Pritekel et al., 2006; Seastedt & Pyšek, 2011). Following initial colonization, the spread/growth of species may also respond to these same ecological drivers (Mack, 2000; Seastedt & Pyšek, 2011).

As many of the same ecological factors that regulate local invasibility may also respond to the invasion, there is the potential for the impacts of the invasion to be contingent on when and where the invading species became established. Here, context dependency occurs when the same controllers of invasion success are also impacted by the invasion. As invasions form a temporal continuum from colonization, to spread to dominance/impact (Seastedt & Pyšek, 2011), linkages across these stages may be common in many ecological systems and may confound estimates of impacts. For

example, if local species richness is negatively correlated with invader cover, it may be the result of local biotic resistance to invasion, invader-generated depression of richness, or both. As long-term data are rare for most systems (Willis et al., 2007), adequately differentiating invasion impacts from patterns of invasion will be difficult.

This project is designed to determine the prevalence of context dependence in the impacts of invasive species on local patterns of colonization. To investigate the context dependency of invasive plants in the Northeast region of the United States, four problematic invasive species were chosen, *Alliaria petiolata*, *Lonicera japonica*, *Microstegium vimineum*, and *Rosa multiflora* (Cheplick, 2005; Pisula & Meiners, 2010; Robertson et al., 1994). I used long-term data from the Buell-Small Succession Study to address the temporal sequence of each invasion to determine the ecological characteristics associated with the ability of each invasive species to establish and spread, as well as to impact the plant community. Specifically, my goals were to: (1) determine the parameters that affect the ability of each invasive species to establish within a plot, (2) determine the parameters that affect the spread/growth of each invasive species, (3) determine the impacts of each invasive species on the local richness and vegetative cover of the community, and (4) relate the impacts of the invasive species to the parameters that effected establishment and growth/spread (*i.e.* context dependency).

Methods

Study Site and Data Collection

The Buell-Small Succession Study, a long-term observational study, was founded in 1958 at the William L. Hutcheson Memorial Forest Center in the Piedmont region of

central New Jersey (Meiners et al., 2015; Pickett, 1982). The study is comprised of 10 agricultural fields abandoned sequentially in pairs, with the initial two fields abandoned in 1958 and the last pair in 1966. Each field contains 48 permanently marked plots (2.0 × 0.5 m). Vegetation in the fields was sampled annually until 1977. After this, fields were sampled biennially with half of the fields being sampled each year, thus completing a full survey every two years. Data collected are the percent cover occupied by each plant species and bare ground. If a plant species is present, but it does not meet the minimum threshold of cover, 1%, then it receives a cover value of 0.1%. These data represent the longest, continuous study of old field succession (Meiners et al., 2015).

Focal Species

We selected four dominant invasive species, *Alliaria petiolata*, *Lonicera japonica*, *Microstegium vimineum*, and *Rosa multiflora*, from the mid- to late-successional phase of the study. These species are all native to the temperate climates of Europe and Asia (Bossdorf et al., 2004; Flory, 2010; Huebner et al., 2014; Schierenbeck et al., 1994). *Alliaria petiolata* colonizes a wide range of wooded habitats and spreads rapidly due to mass production of seeds. Allelopathic chemicals may facilitate invasion by inhibiting the growth/establishment of competitors by altering the composition of soil microbial communities (Bossdorf et al., 2004; Cipollini et al., 2005). *Lonicera japonica*, a liana, is able to establish in open habitats or forests, where it capitalizes on canopy disturbances to rapidly expand (Robertson et al., 1994; Schierenbeck et al., 1994; Ward et al., 2019). *Microstegium vimineum* is a grass with the ability to grow and reproduce in shaded forest understories, and in recently disturbed areas such as floodplains or

abandoned farmland (Cheplick, 2005; McGrath & Binkley, 2009). *Rosa multiflora* has the ability to reproduce by bird-dispersed seed and clonal growth (Jesse et al., 2010; Lundgren et al., 2016); this allows *R. multiflora* to rapidly invade open habitats and forest gaps (Banasiak & Meiners, 2009; Jesse et al., 2010; Robertson et al., 1994). All of these non-native species have become problematic invaders throughout eastern North America and represent major conservation concerns (Belote & Weltzin, 2006; Bossdorf et al., 2004; Cheplick, 2005; Jesse et al., 2010).

Analysis Structure

For each of the four invasive species, I examined the temporal dynamics of the system across the trajectory of invasion for each focal species (Fig. 1.). To do this, I selected a time (T_1) early in the invasion to describe initial plot conditions. I then calculated changes from this initial state to the peak of invasion (T_2). Alternate year sampling necessitated the usage of pairs of sample years to achieve this temporal window. *Lonicera japonica* ($T_1 - T_2$; Age 5/6 – 15/16) and *Rosa multiflora* (Age 10/11 – 20/21) were well established regionally at abandonment and invaded plots as a part of their successional dynamics. Therefore, I used field age to select the temporal window for analysis. However, *Alliaria petiolata* ($T_1 - T_2$; 1990/1991 – 1996/1997) and *Microstegium vimineum* (2001/2002 – 2007/2008) uniformly invaded all fields simultaneously, once they appeared in the region. For these two species, I used calendar year as a more appropriate timestamp for invasion. I specifically avoided a severe drought in 1999, to remove any potentially confounding effects in the impacts of *M. vimineum*.

For each time period selected, I determined the species richness and total cover (summed across species, omitting the invader) of the plots at T_1 and T_2 as the metrics of primary concern. Additionally, I extracted initial (T_1) cover values of the five most abundant associated species, percentage of bare ground, and the abundances of life form (grass, forbs, trees, shrubs, and lianas). I also extracted the initial and final cover for the focal invader to generate a metric for the magnitude of invasion. These data were used to address drivers of three phases of species invasion: initial establishment, spread, and impact (Belote and Weltzin 2006; Lundgren et al 2016).

Initial Establishment of Invasive Species

To determine the factors associated with the pattern of invasive species establishment within the BSS, I examined how latency to invasion was related to plot conditions at T_1 . I used a Cox Regression to relate species richness and total vegetative cover with when a plot was invaded over all temporal samples between the T_1 to T_2 timeframe. I also included other potential drivers of invasion that may be related to invasibility: life form abundances and dominant species cover. Plots already invaded at T_1 were excluded from analyses, thus removing any left censored data.

Spread of Invasive Species

To relate plot conditions at T_1 to the success (increase in cover) of invasive species once established, I implemented a forward stepwise regression. Specifically, I related the change in focal species' cover between T_1 and T_2 to initial plot conditions (species richness, total cover, life form abundance, and the abundances of dominant

species). Each of the aforementioned parameters were $\log(x+1)$ transformed to improve normality of residuals. Plots in this analysis were restricted to those that were not colonized at T_1 and those that became invaded by T_2 so that invasion success was not confounded by the pattern of colonization.

Temporally Explicit Impacts of Invasion

To determine invasion impacts on the community metrics of interest, species richness and total cover, I related changes between T_1 and T_2 to the success of the invader. I categorized all plots into four invasion classes based on the cover of the focal invasive species at T_2 : uninvaded (0%), low (0.1-33%), moderate (34-66%), and high (67-100%). I then utilized ANOVA to determine whether there were significant impacts of invasion class on the change ($T_2 - T_1$) in species richness or total cover over each species' timeframe. Changes that occurred in uninvaded plots represent dynamics of the system external to the invasion (*i.e.* succession). Plots invaded at T_1 were excluded from analyses, thus removing left censored data.

Temporally Static Impacts of Invasion

To assess whether context dependent analyses yielded different estimates of invasion impacts, I also implemented temporally static (T_2) analyses on the impacts of invasion regarding species richness. This approach mimics, single-time sampling efforts to detect impacts, although our data benefitted from knowing when the invasion peaked. The same invasion classes as above were utilized in these analyses, using all plots. I then

used an ANOVA to determine the significance of the impacts by each invasion class on species richness at T₂.

Results

Initial Establishment of Invasive Species

The models produced here detailing the establishment of invasive species are illustrated in Fig. 2. During the invasion timespan, *Alliaria petiolata* became established in 39.5% (162/461) of the plots not invaded at T₁. Several variables were significantly associated with the latency of a plot becoming invaded by *A. petiolata* (overall model $P < 0.0001$, $df = 12$). Initial species richness ($\exp(\beta) = 0.9274$, $P = 0.0006$) as well as the cover of three prevalent species *Lonicera japonica* ($\exp(\beta) = 0.9825$, $P = 0.0014$), *Cornus florida* ($\exp(\beta) = 0.9902$, $P = 0.0058$), and *Juniperus virginiana* ($\exp(\beta) = 0.9902$, $P = 0.0265$) were all significantly associated with a decreased likelihood of invasion by *A. petiolata*.

Lonicera japonica invaded 51.7% (240/464) of the plots surveyed from T₁ to T₂ and produced a significant model of latency to invasion (overall model $P < 0.0001$, $df = 12$). Initial species richness ($\exp(\beta) = 1.092$, $P = 0.0003$), as well as abundances of three prevalent species at T₁, *Dactylis glomerata* ($\exp(\beta) = 1.017$, $P = 0.0084$), *Aster pilosus* ($\exp(\beta) = 1.022$, $P < 0.0001$), and *Elytrigia repens* ($\exp(\beta) = 1.019$, $P = 0.0023$) were associated with an increased the risk of invasion by *L. japonica*.

During the invasion timespan, *Microstegium vimineum* colonized 83.9% (282/336) of the plots uninvaded at T₁ with two initial plot variables that were significantly associated with the risk of invasion (overall model $P < 0.0001$, $df = 12$).

Initial species richness ($\exp(\beta) = 1.078$, $P = 0.0004$) increased the risk and shrub cover ($\exp(\beta) = 0.9855$, $P = 0.02491$) decreased the risk of invasion by *M. vimineum*.

Rosa multiflora invaded approximately 56.9% (243/427) of the plots surveyed from T₁ to T₂. However, the Cox Regression did not produce a significant model regarding the risk of invasion by *R. multiflora* (overall model $P = 0.05348$, $df = 12$).

Spread of Invasive Species

The spread of *Alliaria petiolata* was positively associated only with tree cover ($F_{2, 179} = 5.616$, $P = 0.0043$, $R^2 = 0.0590$, $\beta = 0.1303$). In contrast, the spread of *Lonicera japonica* was related to three variables ($F_{4, 235} = 14.72$, $P < 0.0001$, $R^2 = 0.2003$). This model indicated that the amount of cover occupied by *Elytrigia repens* ($P < 0.0001$, $\beta = -0.3723$) and trees ($P = 0.0002$, $\beta = -0.6861$) were negatively associated with the spread of *L. japonica*, whereas bare ground ($P = 0.0220$, $\beta = 0.1889$) was positively associated with *L. japonica* cover increase.

Microstegium vimineum spread was significantly influenced by four variables ($F_{5, 275} = 12.52$, $P < 0.0001$, $R^2 = 0.2146$). The model indicated that the amount of cover occupied by *Juniperus virginiana* ($P < 0.0001$, $\beta = -0.2690$), *Acer rubrum* ($P < 0.0001$, $\beta = -0.1511$), and *Lonicera japonica* ($P = 0.0487$, $\beta = -0.1408$) all were negatively associated with *M. vimineum*, while cover the forb life form ($P = 0.0097$, $\beta = 0.1311$) was positively associated with increase in *M. vimineum*. Despite the lack of association of invasion with local conditions, the spread of *Rosa multiflora* was associated with two plot variables ($F_{2, 240} = 5.267$, $P = 0.0058$, $R^2 = 0.0421$). The spread of *R. multiflora* was

negatively associated with bare ground ($P = 0.0320$, $\beta = -0.2491$) and *Poa pratensis* cover ($P = 0.0160$, $\beta = -0.1502$).

Temporally Explicit Impacts of Invasion

The models produced here detailing the temporally explicit (T_1 - T_2) impacts of invasive species on total vegetative cover and species richness are illustrated in Fig. 2 and Fig. 3. Invasions were significantly associated with changes in species richness and total cover from T_1 to T_2 in three of the four focal species. Plots with greater levels of *Alliaria petiolata* cover showed decreases in species richness, whereas plots that were uninvaded or had low levels of *A. petiolata* increased in species richness from T_1 to T_2 ($F_{3,457} = 3.847$, $P = 0.0097$, $R^2 = 0.0246$). As *A. petiolata* was more likely to invade plots with low species richness, the impacts would differentially impact the poorest richness areas of the BSS. *Alliaria petiolata* also had significant effects on the total cover of plots ($F_{3,457} = 5.406$, $P = 0.0012$, $R^2 = 0.3427$). Plots with moderate to high levels of *A. petiolata* experienced significant decreases in total vegetative cover (excluding the invader), whereas plots that were lightly invaded or uninvaded showed slight increases in total cover over time.

Plots with greater levels of *Lonicera japonica* cover had significant decreases in species richness. However, plots that were uninvaded or had low levels of *L. japonica* slightly increased in species richness from T_1 to T_2 ($F_{3,460} = 23.01$, $P < 0.0001$, $R^2 = 0.1305$). Recall that *L. japonica* had an increased likelihood to invade plots with higher species richness, meaning diverse plots were more likely to be impacted by the species. *Lonicera japonica* significantly impacted the amount of total vegetative cover (excluding

the invader) of plots varying by invasion level ($F_{3,460} = 39.86$, $P < 0.0001$, $R^2 = 0.2063$). Plots with moderate to high levels of *L. japonica* decreased in total vegetative cover whereas plots that were uninvaded or lightly invaded slightly increased in total cover from T_1 to T_2 .

The prevalence of *Microstegium vimineum* did not significantly impact the change in species richness during the timeframe of invasion ($F_{3,332} = 1.457$, $P = 0.2262$, $R^2 = 0.0130$). *Microstegium vimineum* also did not significantly affect changes in total vegetative cover of the plots through time ($F_{3,332} = 0.5272$, $P = 0.6639$, $R^2 = 0.0047$).

Plots invaded by *R. multiflora* showed significantly greater decreases in species richness, relative to uninvaded plots. Interestingly, plots that were uninvaded also showed a decrease in species richness during the timeframe of invasion ($F_{3,423} = 2.894$, $P = 0.0350$, $R^2 = 0.0201$). Plots with high levels of *R. multiflora* showed significant decreases in total vegetative cover when compared to plots that were lightly or moderately invaded or completely uninvaded ($F_{3,332} = 8.794$, $P < 0.0001$, $R^2 = 0.0587$).

Temporally Static Impacts of Invasion

The models produced here detailing the temporally static (T_2) impacts of invasive species are illustrated in Fig. 4. Analyses that ignored the temporal context of invasion yielded different estimates of the impacts of invaders on species richness. Plots that were invaded by *Alliaria petiolata* at any level were shown to have lower species richness than uninvaded plots ($F_{3,476} = 18.51$, $P < 0.0001$, $R^2 = 0.1044$). Plots moderately or highly invaded by *Lonicera japonica* had significantly lower species richness than plots that were uninvaded or lightly invaded ($F_{3,476} = 22.72$, $P < 0.0001$, $R^2 = 0.1253$). In contrast,

plots invaded by *Microstegium vimineum* at a low or moderate level were shown to have significantly greater species richness than uninvaded plots ($F_{3,476} = 10.34$, $P < 0.0001$, $R^2 = 0.0612$). For *Rosa multiflora*, plots that were highly invaded were shown to have significantly lower species richness ($F_{3,476} = 11.39$, $P < 0.0001$, $R^2 = 0.0670$), in contrast to the analysis of change over time.

Discussion

In theory, areas with higher levels of species richness should have more niches filled and should be better able to utilize their resources and thus be more difficult to invade (Meiners et al., 2004). Contrary to diversity-invasibility theory, we found that *Lonicera japonica* and *Microstegium vimineum* showed increased likelihood of establishment in plots with higher species richness. One possible explanation is that higher richness areas were not dominated by one competitively dominant species, allowing invasions to occur more easily. Another possibility is that high richness areas simply have higher resource availability or are otherwise more suitable for a wider range of species. Our study found that only *Alliaria petiolata* fit the conceptual association between species richness and risk of invasion. One plausible explanation is that plots with higher species richness more completely utilize the limiting resources, thus inhibiting the ability of *A. petiolata* to establish (Cipollini et al., 2005; Hale et al., 2016). *Rosa multiflora* did not appear to have any relationship between species richness and likelihood of invasion. However, a less detailed logistic regression of the BSS data found a positive relationship between this species and local richness (Meiners et al., 2004). The

directionality seen in that analysis was consistent with the failure time approach employed here, which did not quite reach statistical significance.

Some life forms and species had clear effects on the ability of the invasive species to establish. *Alliaria petiolata* was inhibited by the presence of *Cornus florida* and *Juniperus virginiana*. These trees may inhibit establishment by reducing light availability or, in the case of *J. virginiana*, by producing a thick, slowly decomposing leaf litter (Bossdorf et al., 2004; Burns & Honkala, 1990a, 1990b). In contrast, plots with high cover of *Dactylis glomerata*, *Symphotrichum pilosum* (syn. *Aster pilosus*), and/or *Elytrigia repens* were positively associated to the risk of establishment by *Lonicera japonica*. It is plausible that the successional collapse of the resident species generated opportunities for the establishment of *L. japonica* (Keever, 1979; Myster & Pickett, 1994; Peterson & Bazzaz, 1978; Stolciová & Honěk, 2018), rather than any direct facilitation. *Microstegium vimineum* invasion was greater in plots with low shrub cover, likely reflecting less competition for light (Cole & Weltzin, 2005). Plots with more bare ground had increased likelihood of invasion by *Rosa multiflora*, likely linked with opportunities for seedling establishment (Banasiak & Meiners, 2009).

In contrast to patterns of initial invasion, neither species richness nor total vegetative cover had significant impacts on the spread of invasive species. Rather, we found that cover of life forms and dominant species were more influential on the spread of invaders. Plots with higher tree cover also developed greater *Alliaria petiolata* cover, likely due to both the displacement of less shade tolerant herbaceous competitors that still persisted in the BSS at that time as well as the species' shade tolerance. We found that plots with high cover of *Elytrigia repens* and trees exhibited significantly lower levels of

Lonicera japonica spread. At year 5, tree cover would have been primarily overhanging canopy from the adjacent forest, and not represent potential host trees. The negative influence of *E. repens* and positive influence of bare ground on *L. japonica* spread further supports this species initial dependence on open habitats and that competition can play a large role in its establishment.

Plots with high cover of *Juniperus virginiana*, *Acer rubrum*, and *Lonicera japonica* showed significantly lower levels of spread by *Microstegium vimineum*, indicating light competition as a potential limiting factor for this invader (Cole & Weltzin, 2005) despite its shade tolerance (Redwood et al., 2018). We also found that areas dominated by forbs showed increased spread of *M. vimineum*, which may be reflective of understory conditions that enable herbaceous community development, perhaps including light availability. Plots dominated by *Poa pratensis*, a highly persistent and competitive grass (White et al., 2013), showed decreased spread of *R. multiflora*. Contrary to its effect on *M. vimineum*, bare ground negatively affected spread of *R. multiflora* suggesting that *R. multiflora* is not a good competitor for bare ground.

Within the temporally-explicit analyses, we found that *Alliaria petiolata*, *Lonicera japonica*, and *Rosa multiflora* all significantly reduced the species richness and total vegetative cover of resident communities, whereas *Microstegium vimineum* showed no detectable impacts. However, there were marked differences in the severity of each invasion's impacts. Plots that were moderately or highly invaded by *A. petiolata* showed large decreases in average total vegetative cover ranging from 20 to 25% in the timeframe of invasion. Similarly, plots that were lightly invaded by *A. petiolata* experienced slight increases in species richness, whereas plots that were moderately or

heavily invaded were negatively affected. These impacts may be due to the allelopathic nature of *A. petiolata* (Hale et al., 2016; Pisula & Meiners, 2010). *Microstegium vimineum* may have failed to show significant impacts on species richness and total vegetative cover due to its temporal proximity to the invasion and impacts of *A. petiolata*. It is also plausible that fewer interactions are occurring due to the underdeveloped understory community. Plots that were moderately or highly invaded by *L. japonica* showed significant decreases in both species richness and total vegetative cover, whereas those that were uninvaded or lightly invaded showed slight increases. The impacts of *L. japonica* may be attributed to its competitive ability.

Plots invaded by *R. multiflora* overall had decreases in species richness, however the level of invasion was not statistically significant due to high variation. *Rosa multiflora* showed greater impacts on total vegetative cover where higher levels of invasion clearly decreased the amount of vegetation in invaded plots. We found that species richness was clearly impacted in 3/4 invasions using temporally-explicit data. In comparison, total vegetative cover seems to have been more influenced by the level of dominance exhibited by invaders, shown by three of the four invasive species having statistical significance between Uninvaded-Moderate/High.

There were several situations where the impacts on invasion may have been modified by the context of the initial invasion and spread. *Alliaria petiolata* preferentially invaded plots with lower levels of species richness and through its invasion further decreased the species richness of the area. In this situation context dependency had the potential to artificially amplify the magnitude of impact. In contrast, both *Lonicera japonica* and *Microstegium vimineum* had increased likelihood of invasion in plots with

high initial species richness. Plots invaded by *L. japonica* subsequently had decreases in species richness, offsetting the initial pattern of colonization. In contrast, invasions by *M. vimineum* did not impact local species richness, but an association with richness may persist from the pattern of invasion. As total cover was not significantly related to the establishment or spread of any species, impacts on that community metric should not be context dependent.

Ultimately, the conservation implications of context dependency rely on whether the magnitude of impacts detected from single-time surveys are biased by their context dependency on the patterns of invasion. The comparisons here refer to Fig. 5, which shows the temporally explicit (T_1 - T_2) and static (T_2) impacts of each invasive species on species richness. The temporally static analysis consistently underestimated the impacts of *Lonicera japonica* by an average of 2 species when compared to the temporally explicit analysis, showing that accounting for context dependence may produce more robust analyses. Within the static analysis, the impacts of *L. japonica* in areas that were moderately and highly invaded were underestimated by approximately 38% and 33%, respectively.

In contrast, the temporally static analysis for *Alliaria petiolata* overestimated the impacts made by the invasive species and the overestimates vary from 74% (-2.5 species) to 161% (-2.3), at high and low levels of invasion respectively. The static analysis for *Rosa multiflora* produced mixed results. It showed success regarding change of species richness in areas that were lightly invaded with a difference of only 0.57 species (context dependent – a loss of 0.11 species, static a gain of 0.46) and to a lesser degree areas that were highly invaded with an overestimate of 26% (-0.74 species). However, the loss of

species richness was underestimated by 89% (1.9 species) in areas that were moderately invaded.

The static analysis of *Microstegium vimineum* indicated increases in species richness in areas that were invaded. These were markedly different than the temporally explicit analysis which showed no impacts on species richness. The static analysis indicated increases in species richness of 1.1 species in lightly invaded areas, 3.2 species in moderately invaded areas, and 1.8 species in highly invaded areas.

Conclusion

These data indicate that establishment and spread of invasive species can be significantly affected by the abundance of dominant species, life forms and the amount of available bare ground in addition to species richness. These local community attributes play an integral role in the establishment of invasive species as they are indicative of the soil nutrients, light levels, and niches available. Thus, we can utilize this information to determine the likelihood of establishment and spread by the invasive species. These attributes also form a critical context for any subsequent impacts of the invader on the community.

As local species richness is one of the key associates of local colonization probability and the primary reason for concern about the impacts of plant invasions, I show that the impacts of invasive species can be significantly confounded by the species richness of the invaded area. However, the relationship appears to be complex as it differs across invaders in direction and magnitude. Not accounting for patterns of invasion significantly altered estimates of impact strength and direction. So, excluding information

on controllers of invasive establishment and spread in assessing invasive species impacts is greatly problematic. While long-term data are not available for most systems, we must be cautious when interpreting single-time studies to assess invaders impacts (Willis et al., 2007).

Literature Cited

- Aguilera, A. G., Alpert, P., Dukes, J. S., & Harrington, R. (2010). Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biological Invasions*, *12*(5), 1243–1252. <https://doi.org/10.1007/s10530-009-9543-z>
- Banasiak, S. E., & Meiners, S. J. (2009). Long term dynamics of *Rosa multiflora* in a successional system. *Biological Invasions*, *11*(2), 215–224. <https://doi.org/10.1007/s10530-008-9226-1>
- Belote, R. T., & Weltzin, J. F. (2006). Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest. *Biological Invasions*, *8*(8), 1629–1641. <https://doi.org/10.1007/s10530-005-3932-8>
- Bossdorf, O., Schröder, S., Prati, D., & Auge, H. (2004). Palatability and tolerance to simulated herbivory in native and introduced populations of *Alliaria petiolata* (Brassicaceae). *American Journal of Botany*, *91*(6), 856–862. <https://doi.org/10.3732/ajb.91.6.856>
- Burns, R. M., & Honkala, B. H. (1990a). Silvics of North America: Volume 1. Conifers. In *Agriculture Handbook 654* (Vol. 1). http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm
- Burns, R. M., & Honkala, B. H. (1990b). Silvics of North America: Volume 2. Hardwoods. In *Agriculture Handbook 654* (Vol. 2). http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm
- Cheplick, G. P. (2005). Biomass partitioning and reproductive allocation in the invasive, cleistogamous grass *Microstegium vimineum*: Influence of the light environment. *The Journal of the Torrey Botanical Society*, *132*(2), 214–224.

[https://doi.org/10.3159/1095-5674\(2005\)132\[214:bparai\]2.0.co;2](https://doi.org/10.3159/1095-5674(2005)132[214:bparai]2.0.co;2)

Cipollini, D., Mbagwu, J., Barto, K., Hillstrom, C., & Enright, S. (2005). Expression of constitutive and inducible chemical defenses in native and invasive populations of *Alliaria petiolata*. *Journal of Chemical Ecology*, *31*(6), 1255–1267.

<https://doi.org/10.1007/s10886-005-5284-3>

Cole, P. G., & Weltzin, J. F. (2005). Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. *Biological Invasions*, *7*(3), 477–488.

<https://doi.org/10.1007/s10530-004-5171-9>

Flory, S. L. (2010). Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restoration Ecology*, *18*(1), 103–112.

<https://doi.org/10.1111/j.1526-100X.2008.00425.x>

Hale, A. N., Lapointe, L., & Kalisz, S. (2016). Invader disruption of belowground plant mutualisms reduces carbon acquisition and alters allocation patterns in a native forest herb. *New Phytologist*, *209*(2), 542–549. <https://doi.org/10.1111/nph.13709>

Huebner, C. D., Steinman, J., Hutchinson, T. F., Ristau, T. E., & Royo, A. A. (2014). The distribution of a non-native (*Rosa multiflora*) and native (*Kalmia latifolia*) shrub in mature closed-canopy forests across soil fertility gradients. *Plant and Soil*, *377*(1–2),

259–276. <https://doi.org/10.1007/s11104-013-2000-x>

Ibáñez, I., Silander, J. A., Allen, J. M., Treanor, S. A., & Wilson, A. (2009). Identifying hotspots for plant invasions and forecasting focal points of further spread. *Journal of Applied Ecology*, *46*(6), 1219–1228. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2009.01736.x)

[2664.2009.01736.x](https://doi.org/10.1111/j.1365-2664.2009.01736.x)

Jesse, L. C., Nason, J. D., Obrycki, J. J., & Moloney, K. A. (2010). Quantifying the levels

- of sexual reproduction and clonal spread in the invasive plant, *Rosa multiflora*. *Biological Invasions*, 12(6), 1847–1854. <https://doi.org/10.1007/s10530-009-9596-z>
- Keever, C. (1979). Mechanisms of Plant Succession on Old Fields of Lancaster County , Pennsylvania. *Bulletin of the Torrey Botanical ClubTorrey Botanical Society*, 106(4), 299–308.
- Lankau, R. (2010). Soil microbial communities alter allelopathic competition between *Alliaria petiolata* and a native species. *Biological Invasions*, 12(7), 2059–2068. <https://doi.org/10.1007/s10530-009-9608-z>
- Lundgren, M. R., Small, C. J., & Dreyer, G. D. (2016). Influence of Land Use and Site Characteristics on Invasive Plant Abundance in the Quinebaug Highlands of Southern New England. *Northeastern Naturalist*, 11(3), 313–332.
- Mack, R. N. (2000). Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions*, 2(2), 111–122. <https://doi.org/10.1023/A:1010088422771>
- Mack, R. N., & Erneberg, M. (2002). The United States Naturalized Flora : Largely the Product of Deliberate. *Annals of the Missouri Botanical Garden*, 89(2), 176–189.
- McGrath, D. A., & Binkley, M. A. (2009). *Microstegium vimineum* Invasion Changes Soil Chemistry and Microarthropod Communities in Cumberland Plateau Forests . *Southeastern Naturalist*, 8(1), 141–156. <https://doi.org/10.1656/058.008.0113>
- Meiners, S. J., Cadenasso, M. L., & Pickett, S. T. A. (2004). Beyond biodiversity: Individualistic controls of invasion in a self-assembled community. *Ecology Letters*, 7(2), 121–126. <https://doi.org/10.1111/j.1461-0248.2003.00563.x>
- Meiners, S. J., Pickett, S. T. A., & Cadenasso, M. L. (2015). An integrative approach to

- successional dynamics: Tempo and mode of vegetation change. In *An Integrative Approach to Successional Dynamics: Tempo and Mode of Vegetation Change*.
<https://doi.org/10.1017/CBO9780511844218>
- Myster, R. W., & Pickett, S. T. A. (1994). A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology*, *75*(2), 387–392.
<https://doi.org/10.2307/1939542>
- Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., Von Holle, B., Moyle, P. B., Byers, J. E., & Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, *1*(1), 3–19.
<https://doi.org/10.1023/A:1010034312781>
- Peterson, D. L., & Bazzaz, F. A. (1978). Life Cycle Characteristics of *Aster Pilosus* in Early Successional Habitats. *Ecology*, *59*(5), 1005–1013.
<https://doi.org/10.2307/1938552>
- Pickett, S. T. A. (1982). Population patterns through twenty years of oldfield succession. *Vegetatio*, *49*(1), 45–59. <https://doi.org/10.1007/BF00051566>
- Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3 SPEC. ISS.), 273–288.
<https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Pisula, N. L., & Meiners, S. J. (2010). Relative allelopathic potential of invasive plant species in a young disturbed woodland 1. *The Journal of the Torrey Botanical Society*, *137*(1), 81–87. <https://doi.org/10.3159/09-ra-040.1>

- Pritekel, C., Whittemore-Olson, A., Snow, N., & Moore, J. C. (2006). Impacts from invasive plant species and their control on the plant community and belowground ecosystem at Rocky Mountain National Park, USA. *Applied Soil Ecology*, *32*(1), 132–141. <https://doi.org/10.1016/j.apsoil.2005.01.010>
- Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- Redwood, M. E., Matlack, G. R., & Huebner, C. D. (2018). Seed Longevity and Dormancy State Suggest Management Strategies for Garlic Mustard (*Alliaria petiolata*) and Japanese Stiltgrass (*Microstegium vimineum*) in Deciduous Forest Sites. *Weed Science*, *66*(2), 190–198. <https://doi.org/10.1017/wsc.2017.74>
- Robertson, D. J., Robertson, M. C., & Tague, T. (1994). Colonization dynamics of four exotic plants in a northern Piedmont natural area. *Bulletin of the Torrey Botanical Club*, *121*(2), 107–118. <https://doi.org/10.2307/2997162>
- Schierenbeck, K. A., Mack, R. N., & Sharitz, R. R. (1994). Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, *75*(6), 1661–1672. <https://doi.org/10.2307/1939626>
- Seastedt, T. R., & Pyšek, P. (2011). Mechanisms of Plant Invasions of North American and European Grasslands. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 133–153. <https://doi.org/10.1146/annurev-ecolsys-102710-145057>
- Simpson, A., & Eyler, M. C. (2018). First Comprehensive List of Non-Native Species

Established in Three Major Regions of the United States. *U.S. Geological Survey Open-File Report*.

- Stolciová, J., & Honěk, A. (2018). Early weed succession on an abandoned field: vegetation composition and production of biomass. *Plant Protection Science*, 35(No. 2), 71–76. <https://doi.org/10.17221/9679-pps>
- Ward, E. B., Pregitzer, C. C., Kuebbing, S. E., & Bradford, M. A. (2019). Invasive lianas are drivers of and passengers to altered soil nutrient availability in urban forests. *Biological Invasions*, 22(3), 935–955. <https://doi.org/10.1007/s10530-019-02134-2>
- White, S. R., Tannas, S., Bao, T., Bennett, J. A., Bork, E. W., & Cahill, J. F. (2013). Using structural equation modelling to test the passenger, driver and opportunist concepts in a *Poa pratensis* invasion. *Oikos*, 122(3), 377–384. <https://doi.org/10.1111/j.1600-0706.2012.20951.x>
- Willis, K. J., Araújo, M. B., Bennett, K. D., Figueroa-Rangel, B., Froyd, C. A., & Myers, N. (2007). How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1478), 175–186. <https://doi.org/10.1098/rstb.2006.1977>
- Yurkonis, K. A., Meiners, S. J., & Wachholder, B. E. (2005). Invasion impacts diversity through altered community dynamics. *Journal of Ecology*, 93(6), 1053–1061. <https://doi.org/10.1111/j.1365-2745.2005.01029.x>

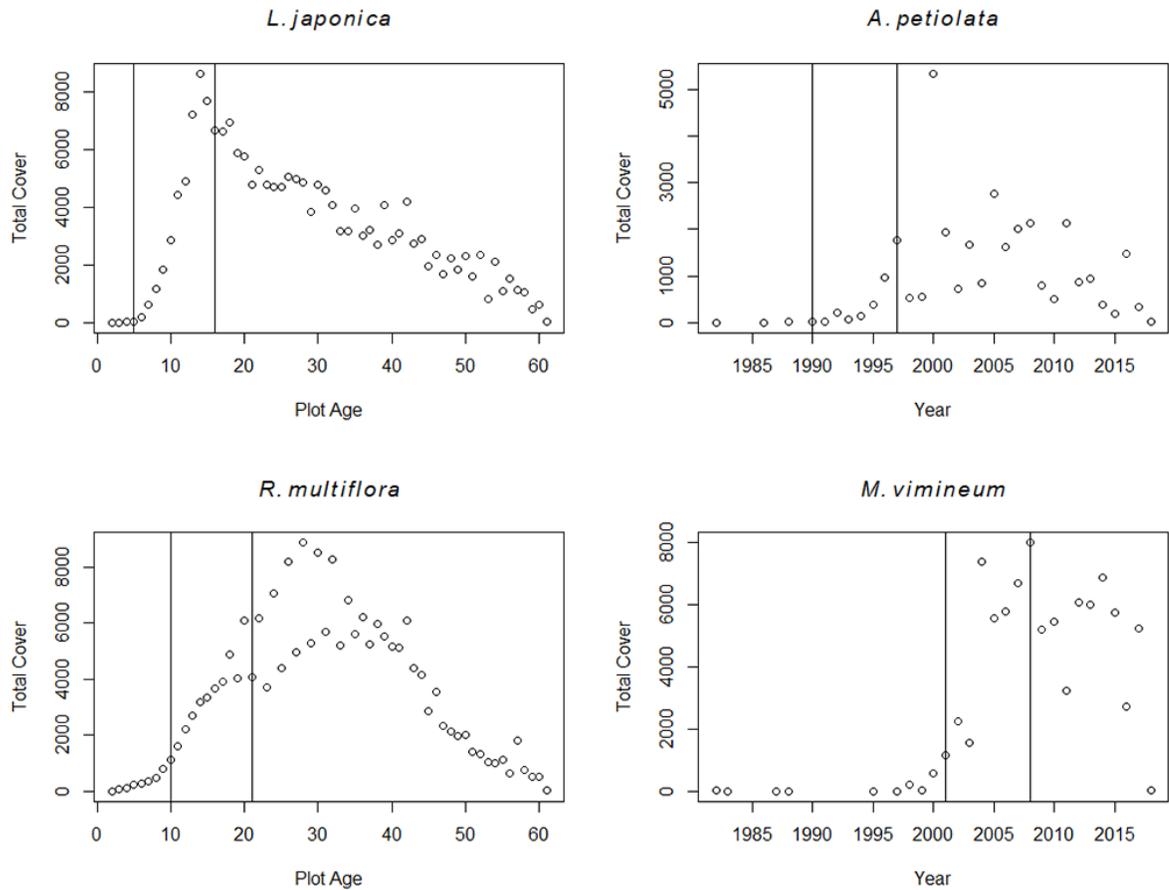


Figure 1: Invasion trajectories of the four focal invasive species for this study. Data plotted are mean cover of the specified species as a function of age/calendar year. Vertical lines represent the timeframe of invasion, T_1 (initial) and T_2 (peak). Species plotted on the left indicate invasion as a function of plot age, those to the right show forest understory invaders as a function of calendar year.

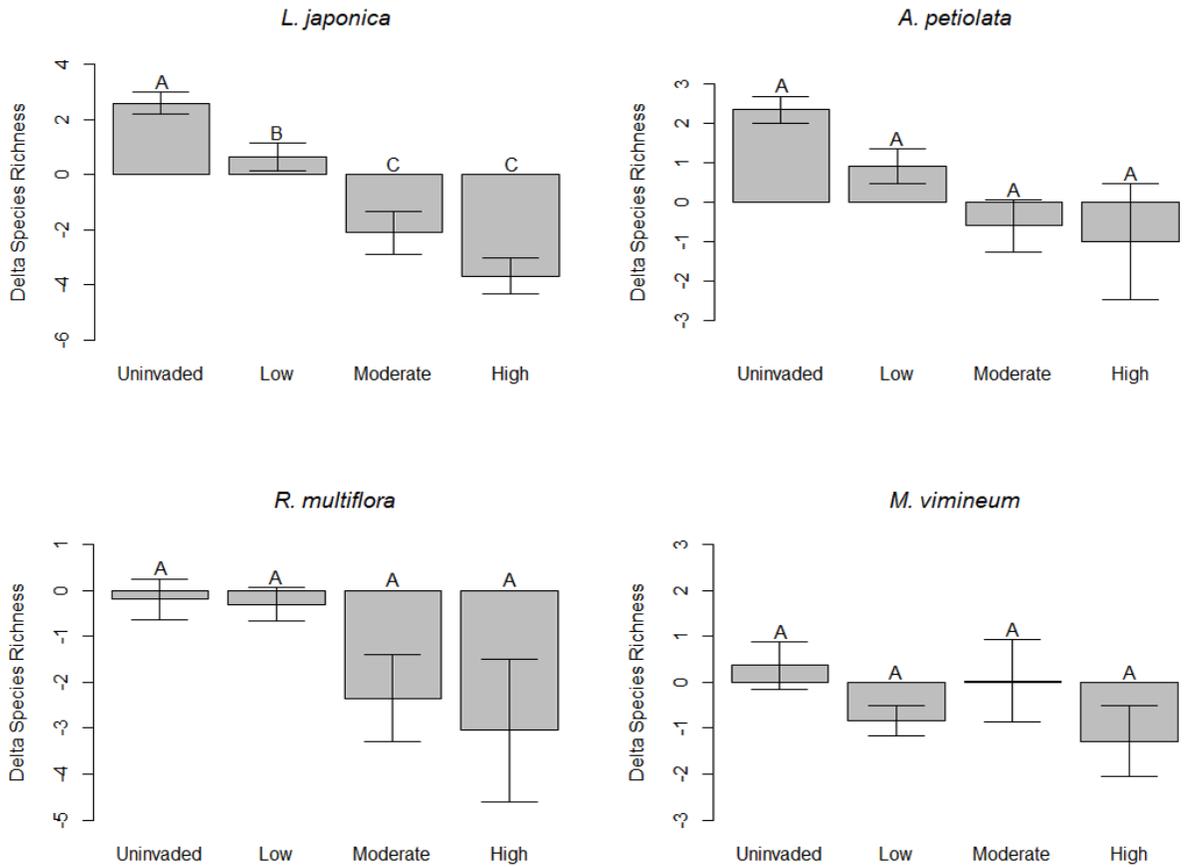


Figure 2: The impact of each focal species on the species richness by invasion class from T_1 to T_2 . Analyses included only plots that were uninvaded at T_1 . Data plotted are means \pm standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.

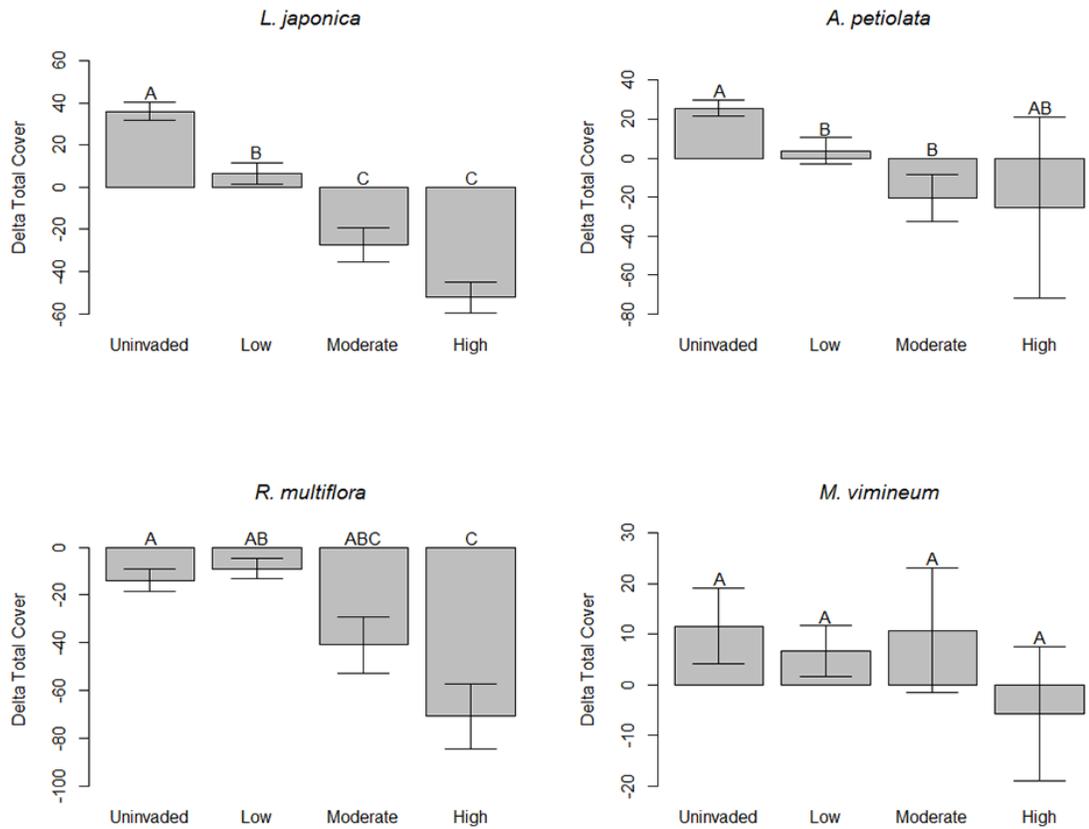


Figure 3: The impact of each focal invasive species on the total vegetative cover by invasion class from T_1 to T_2 . Analyses included only plots that were uninvaded at T_1 . Data plotted are means \pm standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.

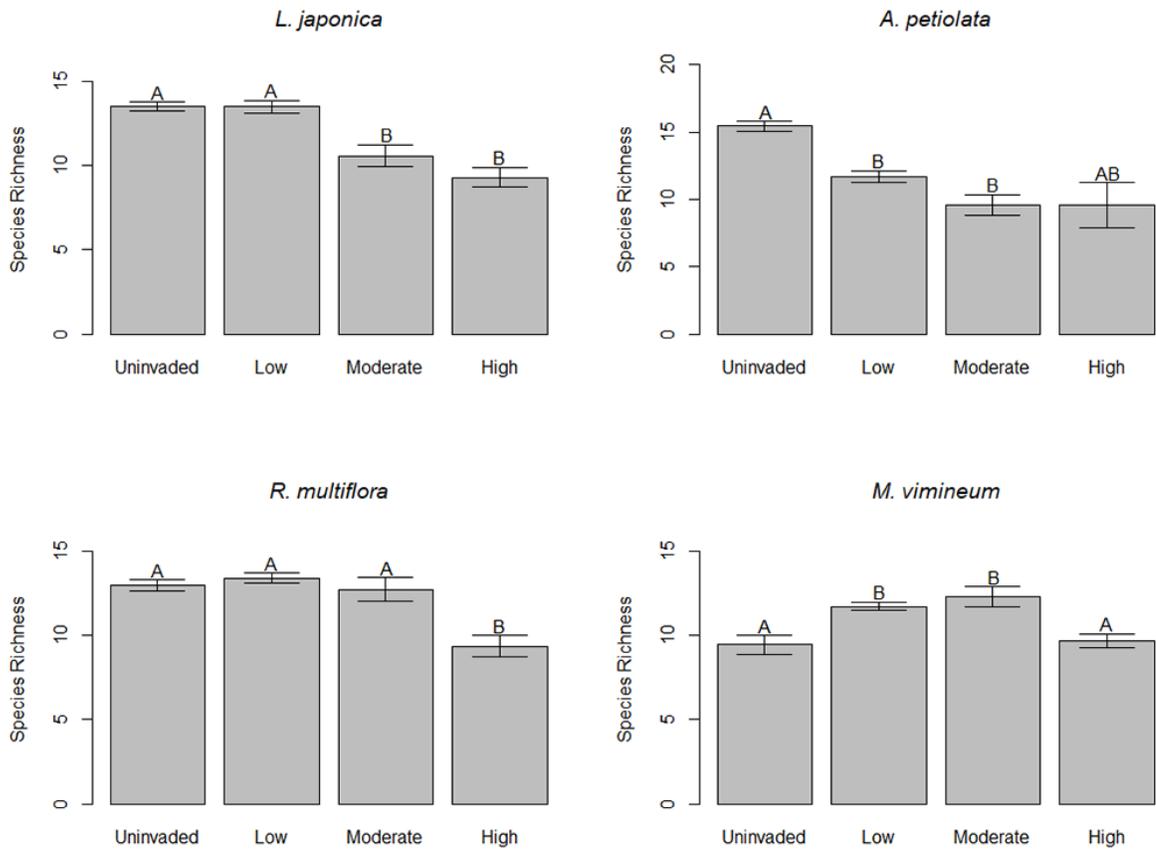


Figure 4: The impact of each focal invasive species on species richness by invasion class at T_2 . Analyses included only plots at T_2 . Data plotted are means \pm standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.

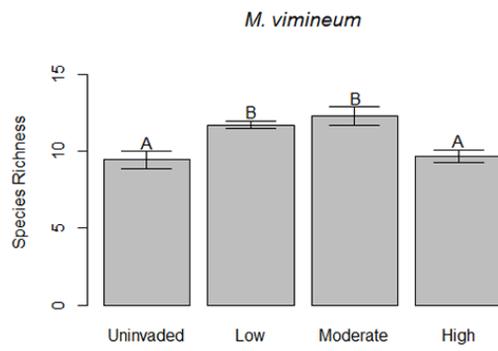
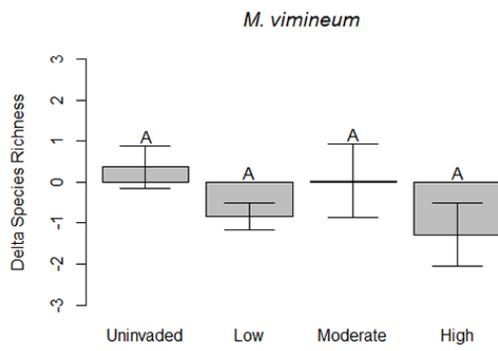
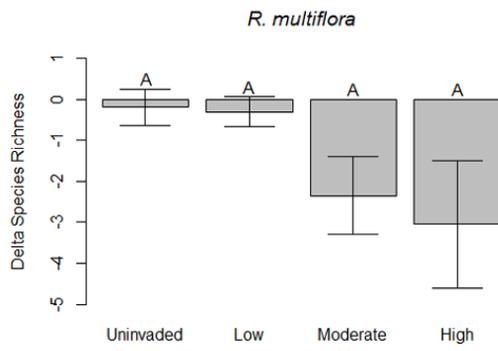
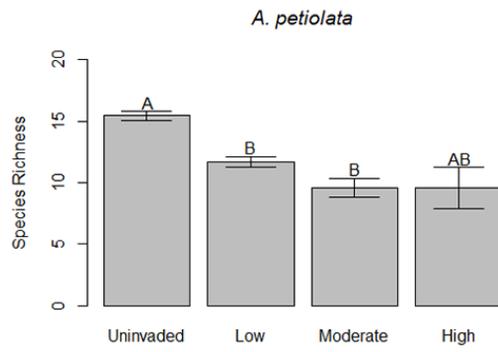
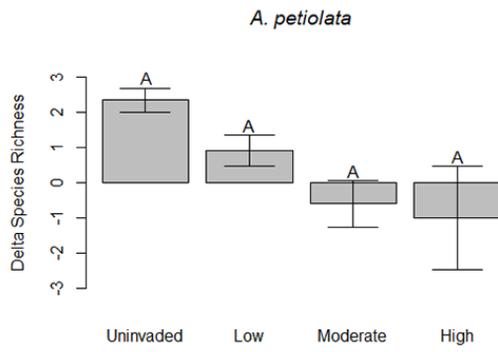
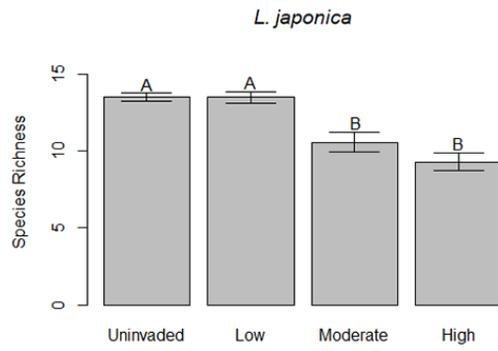
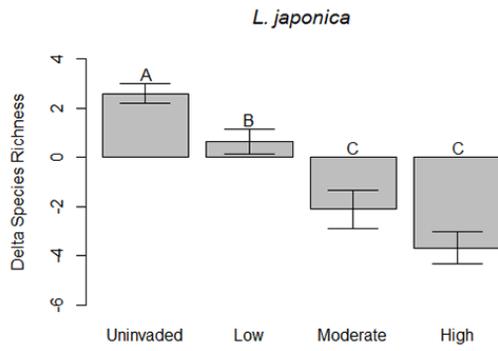


Figure 5: The impact of each focal invasive species on species richness by invasion class of both the temporally explicit (T_1 - T_2) and static (T_2) analyses. Data plotted are means \pm standard error; bars sharing the same letters were not significantly different according to a Tukey HSD test.